Impacts of Simulated Warming on Plant-pollinator Interactions and Ecosystem Services in Agro-ecosystems

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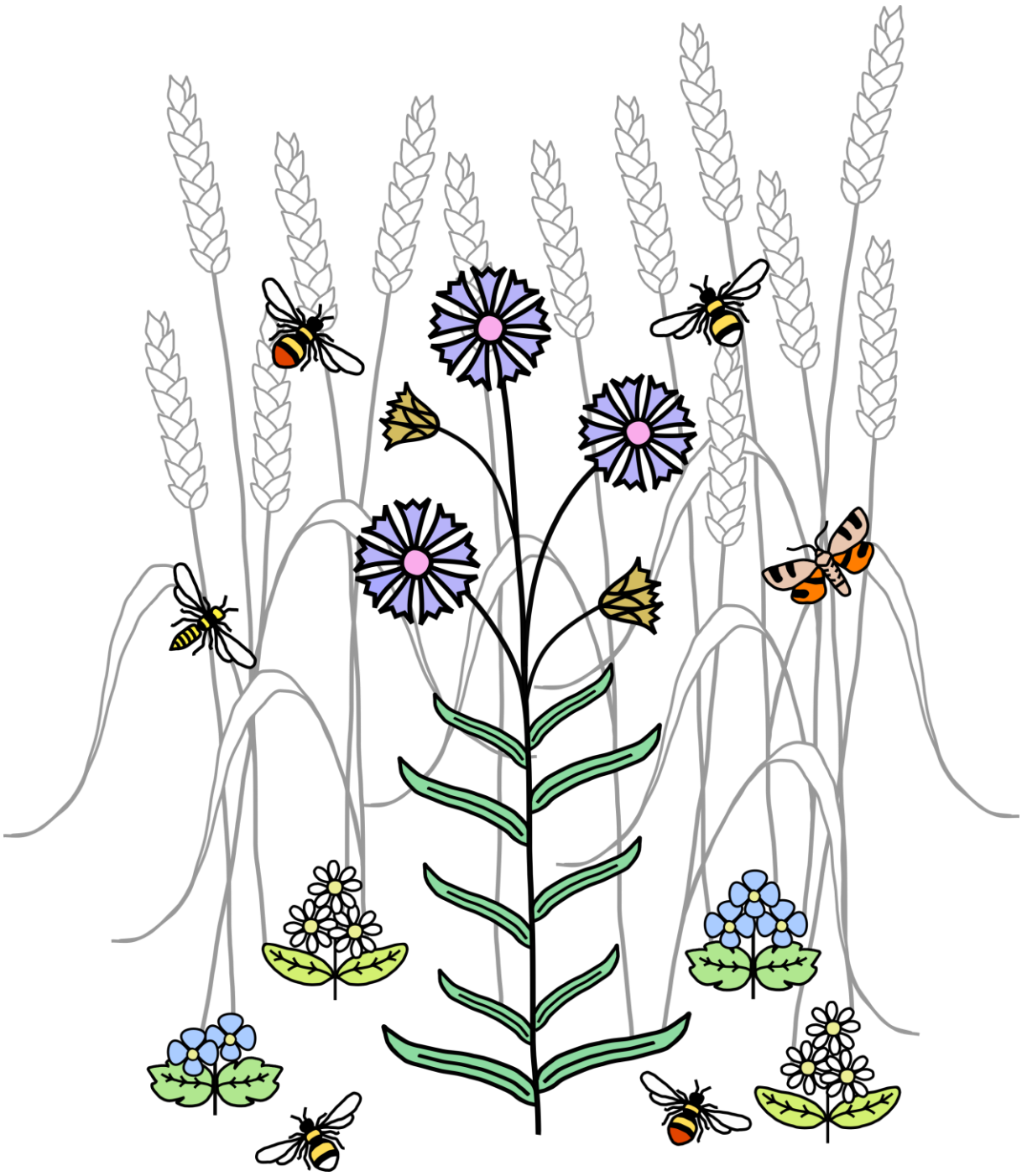

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Abstract

Agro-ecosystems are complex environments that provide a range of ecosystem services, many of which are delivered by biodiversity. Climate change represents a threat to the stability and functioning of agro-ecosystems through the effect it will have on these organisms. This thesis examines the impacts of climate change upon biodiversity in UK agro-ecosystems using both a multidisciplinary framework and a field experiment.

The Driver-Pressure-State-Impact-Response (DPSIR) framework is a problem structuring tool; here it was employed to collate evidence of the impacts of all aspects of climate change on three groups of service providing organisms (pollinators, pest regulators and mycorrhizal fungi) in UK agro-ecosystems, along with evidence linking these effects to societal impacts. Further development of the framework demonstrated downward trends in biodiversity and ecosystem services due to climate change and exposed the lack of evidence examining the effects on species interactions for the three groups.

Climate warming was simulated in a replicated open-air field experiment on an arable farm, where the impacts upon pollinators and wildflowers were investigated. Simulated warming reduced floral abundance by nearly 40% and nectar volumes for two species by over 60%. It also significantly increased the frequency of insect visits to flowers and the complexity of flower-visitor interaction networks. Four of the five wildflower species produced significantly fewer and/or lighter seeds under simulated warming.

Experimental data were collected throughout two growing seasons allowing investigation of both the temporal dynamics of the system and how this responds to simulated warming. Treatment effects on floral abundance, species interactions, and community composition were highly variable throughout the seasons and between years.

Overall, these results suggest that climate change will negatively impact ecosystem service provision in UK agro-ecosystems. More specifically, these findings illustrate the adverse effects that climate change could have upon arable wildflowers and the pollinators that feed upon them.

Author Contributions

I declare that the work herein is intellectually my own. Contributions were made to each data chapter by my supervisors (Darren Evans: DME, Jonathan Atkins: JA) and collaborators (Stéphane Derocles: SD, Aifionn Evans: AE, Robert Jacques: RJ).

Chapter 1

I wrote this chapter with some guidance from DME.

Chapter 2

I conducted the literature review, constructed the framework, and wrote this chapter under the guidance of JA. DME provided some initial suggestions and comments at the end. We aim to publish this chapter as: Moss, E. D., Evans, D. M. and Atkins, J. A. (2019).

Chapter 3

The setup for the simulated warming experiment was co-designed by DME and SD before I started my PhD. I designed and ran the pollinator experiments. I conducted the vast majority of the fieldwork and laboratory work, with some help from AE and RJ. I conducted all data analysis with advice from DME. I wrote the chapter with guidance from DME and made some small changes after receiving comments from an anonymous reviewer for Global Change Biology (the chapter was submitted there in 2017). We aim to publish this chapter as: Moss, E. D. and Evans, D. M. (2019).

Chapter 4

I conducted all data analysis and wrote the chapter with guidance from DME. This chapter was also written with publication in mind, though I am now exploring the possibility of combining the results into the previous chapter to achieve a higher impact paper.

Chapter 5

I wrote this chapter with some guidance from DME.

Dedication

This thesis is dedicated to the NHS and all the members of staff, volunteers and students who keep it running.

Oh, and to Mischief.

Acknowledgements

My supervisors have each provided me with their own brands of help and support, which have collectively made this thesis possible. Darren Evans has been a constant and unswerving source of ecological and methodological advice, a good mentor, and an excellent person to have a good chat/whinge with. Jonathan Atkins helped me to broaden my perspective to include a greater understanding of socio-economics and how it is relevant to ecology. And Gordon Port provided extensive pastoral care and advice relating to my complex health issues, without which I certainly would not have been able to continue with my studies.

There are many people who have helped me with fieldwork or lab work, including my colleagues on the Stockbridge warming experiment: Stéphane Derocles and Sophie Berthe, for their help with setting up and running the experiment, and for teaching me your DNA barcoding method; Aifionn Evans, for your help surveying the plants and pollinators on the farm, counting seeds, and for all that back-breaking hand-weeding; Robert Jacques, for your all-too-brief field assistance, and the thankfully-extensive lab assistance; Bruna Levy Pestana Fernandez, for your willingness to try fieldwork in the UK; and Lindsay Atkinson, for your plant identification assistance, photography, and botanical knowledge. I also need to thank all the staff at Stockbridge Technology Centre, particularly David George and Jennifer Banfield-Zanin. James Kitson has been a veritable fount of entomological and technological knowledge, while Callum Macgregor, Lisa Malm, Rike Bolam and Kirsty Lees have provided valuable advice. All the students and post-docs in Room 5.38 have provided help in some form, at some point. There are also staff and students at Hull University who provided help and support during my time there.

Finally, I owe a great deal to my partner Richard Grant. He has put my career before his own and moved to a completely different region to allow me to conduct this PhD, not once, but twice. He has been an excellent nurse, taxi, and source of laughter during my health difficulties and also provided many nuggets of sage advice relevant to my research. Thanks Ric, for being generally awesome.

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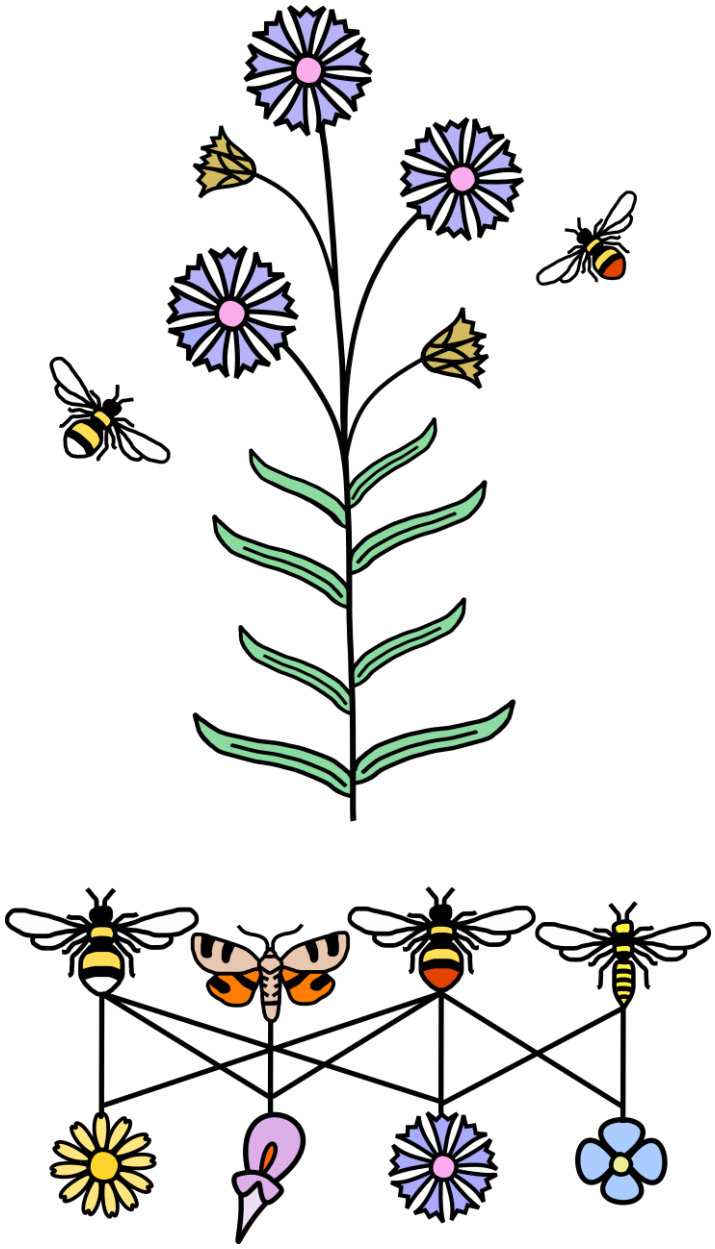
Chapter 1. General Introduction



1.1 Pollinator Importance and Decline

Insect pollinators are a diverse group of animals that includes many thousands of species of wild flies, bees, moths, butterflies and wasps, as well as a small number of domesticated and semi-domesticated bee species. These insects are exceptionally important from an ecological perspective due to them pollinating the vast majority of the world's flowering plants (IPBES, 2017; Ollerton et al., 2011). They are therefore also essential to global agriculture due to the role they play in pollinating flowering crop plants; researchers have previously calculated the global value of insect pollination to be €153 billion (Gallai et al., 2009), and that 35% of global crop production volume was dependant on these animals (Klein et al., 2007). In the UK, around 16% of cropped land grows insect pollinated crops (DEFRA, 2013), and the contribution of insect pollination to crop market value was calculated as £603 million for 2010 (UK NEA, 2011; Vanbergen et al., 2014). The quantity of food produced by pollinators has obvious implications for food security, but their significance to quality is also great; insect pollinated crops are important sources of micro and macro nutrients (Eilers et al., 2011). Crop and wildflower pollination are natural ecosystem processes that can also be considered as 'ecosystem services', that is, they are the benefits that humans gain through normal ecosystem functioning (MEA, 2005). In addition to these biological processes providing us with pollination services, we also receive benefits through cultural processes. Humans have had a close relationship with bees for thousands of years and this is reflected in the art, music, and attitudes of many peoples, including our own modern day Western civilisation (IPBES, 2017). Some examples of how this cultural importance can manifest include: "Flight of the Bumblebee", an extremely popular piece of music composed by Nikolai Rimsky-Korsakov in 1899; the distinctive bee jewellery and hieroglyphs created by the ancient Minoan and Egyptian civilisations thousands of years ago (Ransome, 2004); and the popularity of modern campaigns such as "The Great British Bee Count" by Friends of the Earth (https://friendsoftheearth.uk/bee-count). The presence of pollinators within our environments, and our presence within their environments, provides valuable opportunities for education, recreation, inspiration, and other cultural ecosystem services.

Given the significant roles that insect pollinators play, the recent trends in pollinator declines are alarming as there could be serious implications not only for ecological processes, but also for wider human society. There is a large body of evidence indicating

declines in both the distribution and abundance for a wide variety of pollinator taxa, including: honeybees (Potts et al., 2010), moths (Fox, 2013), butterflies (González-Megías et al., 2008), bumblebees (Kosior et al., 2007), and wild bees and hoverflies (Biesmeijer et al., 2006). These reductions in pollinator abundance and diversity are bound to have negative consequences for the wild and crop plants they pollinate, and the natural, cultural, and agricultural systems they support (Gallai et al., 2009; IPBES, 2017; Lundgren et al., 2016). On-going research into pollinator declines indicates they are being caused by multiple, complex, and interacting factors, but it appears that the main drivers are agricultural intensification, land use change, pesticide use, and disease (Cameron et al., 2011; Kennedy et al., 2013; Senapathi et al., 2017; Tscharntke et al., 2005; Vanbergen and the Insect Pollinators Initiative, 2013; Woodcock et al., 2017). Climate change represents an emerging and unpredictable additional threat to pollinator populations, which is expected to cause further disturbance to insect pollinators and the pollination and cultural services they provide.

1.2 Climate Change

By the end of the 21st century, and relative to records between 1850-1900, global surface temperature change is likely to exceed 1.5 °C, precipitation patterns will be significantly altered, extreme weather events will increase in severity and frequency, and atmospheric CO_2 concentration is predicted to increase (IPCC, 2013). Climate change poses a significant threat to the stability and functioning of all ecosystems, and there is a very strong body of evidence demonstrating the effects it has already had. Research shows that species from a wide range of taxa, including trees; herbs; birds; mammals; reptiles; and insects, have been responding to climatic changes by moving to higher latitudes and higher altitudes, and by advancing phenology (Parmesan, 2006). Unfortunately, distribution changes are problematic for several reasons: vulnerable species may be moving outside of protected areas; habitat fragmentation may impede, and in severe cases prevent, species moving to more optimal climatic conditions; species on islands or at the end of a land mass may have no means to disperse elsewhere; and similarly, montane species may also have no ability to disperse to other high-altitude environments. Phenological advancements can also be challenging where it results in temporal mismatches between species that interact with one another in some manner. Climate change has caused reductions in abundance for many species and even extinctions for some (Parmesan, 2006).

Pollinating insects are susceptible to climate warming induced changes in both distribution and phenology. Lepidoptera have been particularly well-studied with respect to range shifts, with data showing northward advancements for many species in countries across Europe (Parmesan, 2006). There is also evidence demonstrating bumblebee species in Europe and North America have exhibited shifts to higher elevations, and range contractions at the southern edge of their distributions, but crucially, have failed to track climate change at the northern edges (Kerr et al., 2015). Phenological advancement is a significant topic in relation to plants and insect pollinators due to the potential for temporal mismatching if they do not advance at the same rate. There is a lot of evidence demonstrating climate warming induced phenological advancements in a wide variety of flowering plant species and taxa all over the planet, including the UK (Fitter and Fitter, 2002; Parmesan, 2006). There is far less published information on the parallel advancements of pollinators, but there is some evidence for hoverflies, bumblebees, honeybees, and butterflies (Hassall et al., 2017; Hegland et al., 2009; Parmesan, 2006). Several studies have found evidence for temporal mismatching between plants and pollinators (Forrest and Thomson, 2011; Kudo and Ida, 2013; Memmott et al., 2007), while others have found plants and pollinators advancing at the same rate (Bartomeus et al., 2013b, 2011; Rafferty and Ives, 2011). There is a great deal we do not know about when and how climate change induced plant-pollinator asynchronies occur, but it does appear that this is partially determined by environmental and physiological factors, including habitat, specialism/generalism, and seasonality (Willmer, 2012). The consequences of such asynchronies have been found to be detrimental for both the plants and the insects; severe fitness losses have been observed in solitary bees (Schenk et al., 2017), model simulations have demonstrated the potential for pollinator extinctions (Memmott et al., 2007), and wildflower fecundity has been shown to decrease (Kudo and Ida, 2013; Thomson, 2010).

There is great potential for plant-pollinator community compositions to be altered as a result of climate change, and such shifts may be greater than expected due to the varying susceptibility of organisms to distribution and phenology changes. Perhaps the most vulnerable groups are those insects with specialist food plants, nesting requirements, and reproductive strategies; indeed, there is evidence from long-term datasets for disproportionate losses of specialist bee species when abundance and species richness decrease, and that this leads to significant changes in community composition (Bartomeus et

al., 2013a; Burkle et al., 2013). Unfortunately, there are two reasons why the findings of many of the studies that have looked at climate change impacts on pollinators might not be representative of a complete community response: firstly, there has been a focus on generalist pollinators (Bartomeus et al., 2011; Forrest and Thomson, 2011; Willmer, 2012); and secondly, most studies have looked at how climate change affects individual species or a subset of wild pollinators (Bartomeus et al., 2011; Hassall et al., 2017; Kerr et al., 2015; Parmesan, 2006). This highlights the need to examine this topic using a community approach, which can capture the full suite of consequences that climate warming can have on entire communities of interacting insects and plants, and the ecosystem services those communities provide. Species interaction networks are a useful tool for examining community-wide impacts of environmental change (Montoya et al., 2006; Tylianakis et al., 2008), which means they should be well-suited for investigating how climate change affects plant-pollinator communities. However, there are currently very few published examples of climate change investigations that have applied a network approach to examine impacts on plant-pollinator interactions.

1.3 Ecological Networks

Interactions between species in different trophic levels can be visualised and examined using ecological networks (Montoya et al., 2006; Pocock et al., 2016). Standard network analysis involves application of mathematical graph theory, where the species can be regarded as 'nodes' and the interactions as 'edges'. The structure and complexity of the network can be characterised by calculating a burgeoning range of 'network descriptors' using equations that involve the nodes and edges in the network. For more rigorous analysis, quantitative versions of network descriptors can be employed that take account of the frequency of the interactions by weighting the edges (Bersier et al., 2002), see Figure 1.1 for an illustration of a network in both qualitative and quantitative format. Some network descriptors reveal readily recognisable features about the community; Generality (G_q) and Vulnerability (V_q) are measures of how specialised the organisms within the upper and lower trophic levels are, respectively. The majority of commonly-employed descriptors describe structural features of the community and interactions that are slightly more intangible, but no less useful from a community ecology perspective; Connectance (C_q) is a measure of structural complexity that examines the number of potential interactions that are realised,

and Interaction Evenness is a measure of structural uniformity that describes the evenness of interaction frequency. There are many more ecologically-relevant network properties that can be interrogated, which allow researchers to select those that are most appropriate and useful for their specific research questions and datasets. The beauty of this approach, and the reason why it is advantageous for examining community-wide responses to environmental change, is that it can capture all the small-scale responses at the species level and combine them to provide specific community-scale responses that are appropriate for the project (Scaven and Rafferty, 2013). In practice, this means that all the changes in species abundance, diversity, phenology and foraging behaviour, which may not by themselves be substantial, can add up to significant community-scale changes that could remain undetected if a network approach were not used.

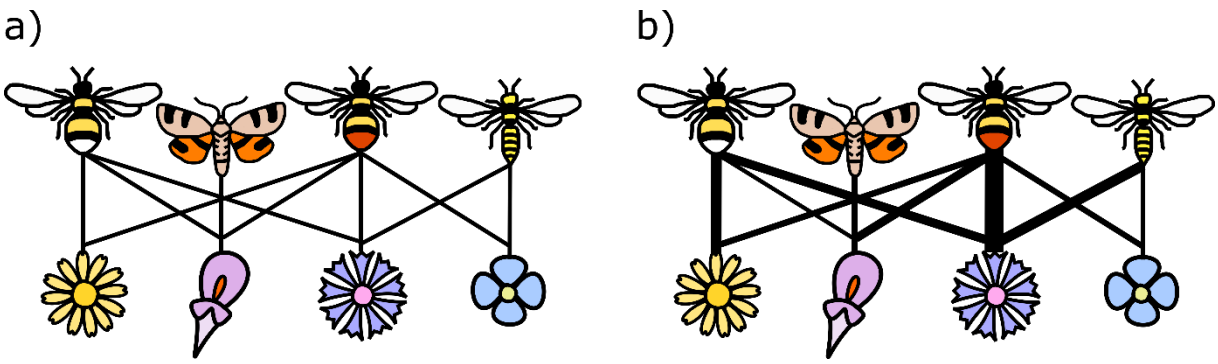


Figure 1.1 Illustration of the difference between qualitative and quantitative networks, using the same example plant-pollinator network; a) a qualitative network where the 'links', or interactions, are unweighted; b) a quantitative network where the links are weighted by the frequency of those interactions.

While there are several published studies that have examined the impacts of climate change on plant-pollinator interactions in a broader methodological context (covered above in section 1.2), there are very few that have specifically constructed and analysed ecological networks of entire communities. Network analysis is a relatively new tool in the field of ecology, which, when combined with the time and resource intensive sampling methods required to generate community-wide species interaction data, can explain the current paucity of studies investigating this specific topic. Memmot et al. (2007) used a modelling approach to investigate how mismatched phenologies could become under increased atmospheric CO_2 concentrations; they found that phenological advancement caused a

reduction in food for pollinators during crucial periods and that this could lead to extinctions of both plants and pollinators. More recently, Burkle et al. (2013) examined historic datasets for changes in plant-pollinator interactions observed over a 120 year period at the same site, which experienced both climatic and land use changes during this time. They found that network structure had been degraded as a result of both temporal and spatial mismatching, and the loss of specialist bee pollinators; they determined that these networks had shown flexibility in response to previous environmental changes but were less resilient to future changes. This study by Burkle et al. (2013) also incorporated a measure of ecosystem function in the form of pollen transfer, which they also found to have degraded over time. Hoiss et al. (2015) used an experimental approach employing an altitudinal gradient as a climate warming proxy in combination with simulated drought and early snow melt treatments to investigate how plant-pollinator network structure could be affected by climate change; they found the degree of network specialisation decreased with increasing elevation, but was only affected by extreme climatic events for generalised networks. The findings of Hoiss et al. (2015) suggest that high generalisation within a network doesn't guarantee stability, but unfortunately they did not assess any measure of ecosystem function. While these three studies have yielded valuable insights on this topic, there is a need for evidence where any relationships between climate change and network structure can be clearly defined. There is also a clear need for more research that includes some form of assessment of ecosystem function.

Examining community structure and function by using a network approach in combination with ecosystem service measurements can provide valuable insights into how climate change may affect plant and pollinator communities and the provision of pollination and cultural services. However, it cannot tell us about what the wider impacts of those changes to biodiversity and ecosystem service delivery may be. The potential for these negative impacts to cascade down into other environmental and societal areas is high, given the importance of these organisms and the services they provide (IPBES, 2017). In order to generate a more complete picture of the issue, additional interdisciplinary methods must be employed that will capture the wider socio-economic situation and consequences.

1.4 The 'Drivers - Pressures - State - Impacts - Response' (DPSIR) Framework

Understanding and managing complex dynamic environments, that include both socio-economic and ecological components, can be aided by the use of inter-disciplinary frameworks or models (Tscherning et al., 2012). These tools vary in their focus and ease of use, which affects their respective suitability to tackling the present topic of climate change impacts upon pollinators. The Outcome Approach has a very strong policy and practical management focus (Olsen, 2003), which makes it less appropriate for investigative applications lead by literature searches. The general framework featured in Ostrom (2009) is more complicated than others, with more categories and far more connections between them, which makes it more difficult for a pure ecologist to apply to a broad topic with sufficient confidence. The Conceptual Framework in the Millennium Ecosystem Assessment (MEA, 2005) has a good focus on ecosystem services and drivers of change, but it lacks sufficient space and structuring for management and policy responses, which are important features of the system in question. The DPSIR framework has been used extensively over the past four decades to investigate, monitor and manage environmental change across a range of systems and problems due to several advantages: it can capture both socio-economic and environmental concerns in equal measure; it has a simple, but comprehensive, structure that indicates causation; and it is easy to populate via a literature review approach (Tscherning et al., 2012). These advantages made the DPSIR the most suitable framework to use in my research.

The DPSIR framework is an information collating and problem structuring approach, which is most often employed to support decision making. The structure of the framework necessitates a focus on the assessment, management, and communication of environmental issues, and dictates a clear portrayal of cause and effect relationships (Tscherning et al., 2012). 'Driving forces' (D) refer to social, economic and environmental drivers of change; these are usually the broad-scale features that are ultimately responsible for change, such as climate change, demand for resources, and population dynamics. 'Pressures' (P) are the specific manifestations of the 'Drivers' upon the system in question; these are the (usually) smaller-scale mechanisms by which change occurs, such as increasing temperature, increased fishing, and increased urbanisation (Gabrielsen and Bosch, 2003). 'State changes' (S) are the observed or predicted changes in the natural environment within the system in question, which occur as a result of the 'Pressures'; these changes could include increased

soil erosion, reduced biodiversity, and habitat loss. 'Impacts' (I) is where the human and social aspects of the system are characterised; this is where the repercussions of the environmental change upon human welfare are detailed, which could include reduced food production, increased resource prices, and reduced benefits from interactions with nature. It is worth noting that while this definition of 'Impacts' is widely accepted amongst socio-economic researchers, some ecological researchers also include environmental considerations here (Holman et al., 2008; Roura-Pascual et al., 2009). 'Responses' (R) are the actions that humans and society put in place in response to the 'Impacts'; these could include both broad- and small-scale measures depending upon the system in question, such as legal changes, government policies, habitat management plans, and agri-environment schemes. Figure 1.2 depicts a simplified DPSIR example that demonstrates the categories and cyclical nature of the framework. Using the DPSIR framework to structure a problem provides a common framework for compilation of issues, requirements, involvement, and advice, from the potentially diverse range of sources and contributors involved (Odermatt, 2004). In doing so, it can aid communication between the different disciplines and bridge the gap between the different stakeholders, policy makers, and their potentially conflicting views (Gabrielsen and Bosch, 2003). Ultimately this means that policy and/or management can be informed by a clear depiction of cause and effect relationships in a way that ensures all interests and parties are considered. There is an additional benefit from using this framework; it can also reveal knowledge gaps and specific areas that require a greater focus, which means the DPSIR is also a useful tool for guiding future research.

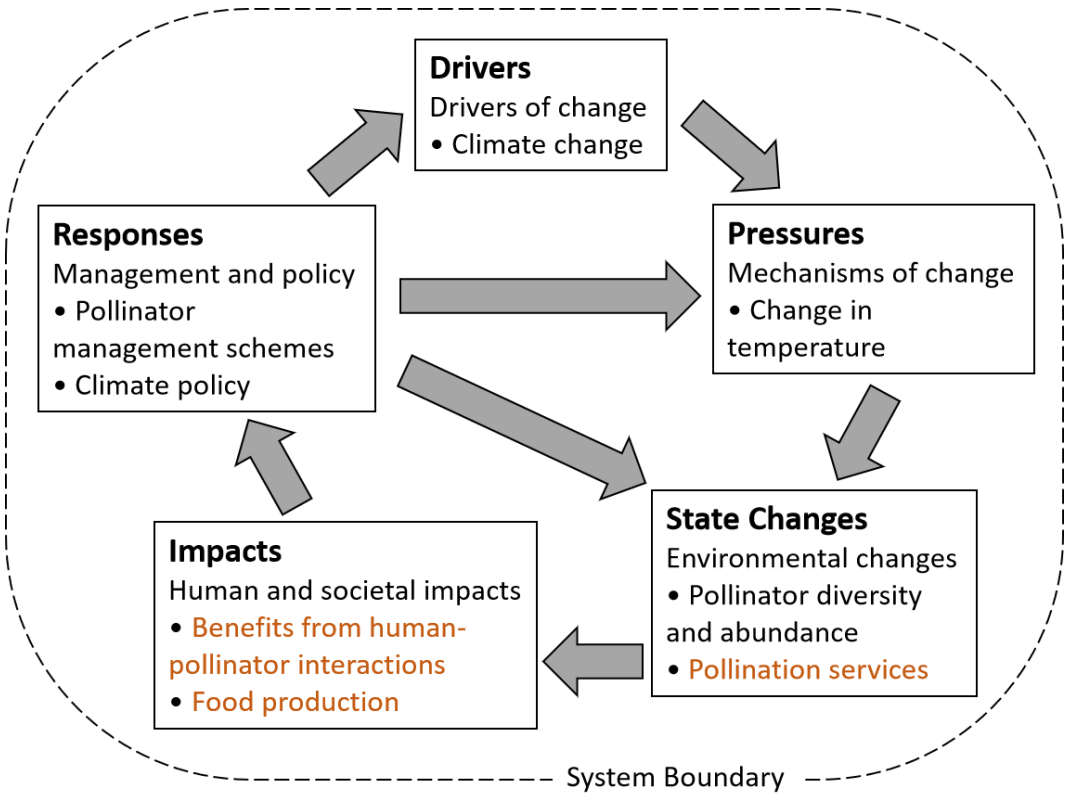


Figure 1.2 Simplified DPSIR framework for climate change impacts on pollinators, including some example features for each category as bullet points. Orange text indicates features that are ecosystem services. Climate change is represented here as a Driver, while the specific aspect of interest (temperature change) is represented as a Pressure.

The creation of a DPSIR comes about through two main methods that may or may not be used in conjunction. The first method involves a thorough investigation of all relevant academic literature, legal acts, policy documents, and management plans; this search must cover all fields and disciplines relevant to the problem, which means it could cover a very broad range of sources and subjects. When used alone, the literature review approach is suited for broad-scale policy applications (Tscherning et al., 2012). The second method involves consultation with experts and stakeholders relevant to the problem who provide their opinions and advice directly to the party creating the DPSIR; this approach usually employs workshops or questionnaires to collect this information. The stakeholder approach is useful for specific, usually smaller-scale, practical applications where the DPSIR framework created will become part of a physical management plan. The presentation of the framework itself varies depending upon the complexity of the problem and system being investigated, but also upon the preferences of the party creating it. Usually, most applications of the framework result in a flowchart, this could be fairly simple (similar to that depicted in Figure

1.2) or quite complex, with some accompanied discussion (Atkins et al., 2011; Gregory et al., 2013), but some researchers choose to discuss their findings without also creating a visual representation of them (Omann et al., 2009).

The DPSIR framework has been applied extensively over the past 20 years to examine many different management problems, most of which related to marine and fresh-water environments (Tscherning et al., 2012). Recently, the use of this framework in terrestrial environments has increased and there is now a diverse range of land-based DPSIR applications covering issues such as soil fertility (Smaling and Dixon, 2006), invasive species (Roura-Pascual et al., 2009), high-altitude agriculture (Lin et al., 2013), and agricultural sustainability (Costantini and Barbetti, 2008). This framework is well-suited to tackling problems relating to environmental change, and many published DPSIR frameworks include climate change as either a 'Driver' (Bär et al., 2015; Holman et al., 2008; Roura-Pascual et al., 2009) or 'Pressure' (Atkins et al., 2011; Elliott, 2011). Another area where the DPSIR framework performs well is consideration of ecosystem services; there are many examples of researchers incorporating ecosystem services into a DPSIR as 'State changes' and/or 'Impacts' (Atkins et al., 2011; Gregory et al., 2013; Pinto et al., 2013), and also in modified categories created specifically to provide a greater focus on ecosystem services (Kelble et al., 2013; Rounsevell et al., 2010). There is one published study where this framework was applied to pollinators; Kuldna et al. (2009) used the DPSIR to examine possible causes for pollinator loss in Europe. While Omann et al. (2009) investigated climate change as a threat to global biodiversity, there are currently no examples in the literature of the DPSIR framework being employed to investigate the specific effects that predicted climate warming will have on biodiversity and ecosystem services in agro-ecosystems.

1.5 Thesis Rationale and Structure

The purpose of this thesis is to conduct some pioneering research that will apply novel approaches to answer some of the questions surrounding the impacts that climate change will have upon plant-pollinator communities and ecosystem services. There were two broad thesis aims: firstly, to conduct some interdisciplinary research that would attempt to provide an overview of the wider impacts of climate change on ecosystem service

delivery; and secondly, to provide the first experimental evidence of how simulated warming affects plant-pollinator interactions and ecosystem function.

1.5.1 Chapter 2: Investigating the impacts of climate change on ecosystem services generated by biodiversity in agro-ecosystems: an application of the DPSIR framework

My first data chapter is an interdisciplinary piece of work carried out under the guidance of my second supervisor, Jonathan Atkins (University of Hull), who is a macro-economist. Here, I employed the DPSIR framework to examine the wider socio-economic impacts that predicted climatic changes could have in UK agro-ecosystems. I reviewed relevant academic literature and policy documents and collated the findings within the framework, before creating two further iterations and combining them into a novel three-step process. Step one is the standard DPSIR format, which takes a broad-scale overview of the whole system and problem; step two is a 'zoomed in' view that shows some of the important relationships in more detail in order to highlight knowledge gaps; step three is a stripped down version that presents directions of change for each feature and service within the DPSIR, based upon current literature and climate projections.

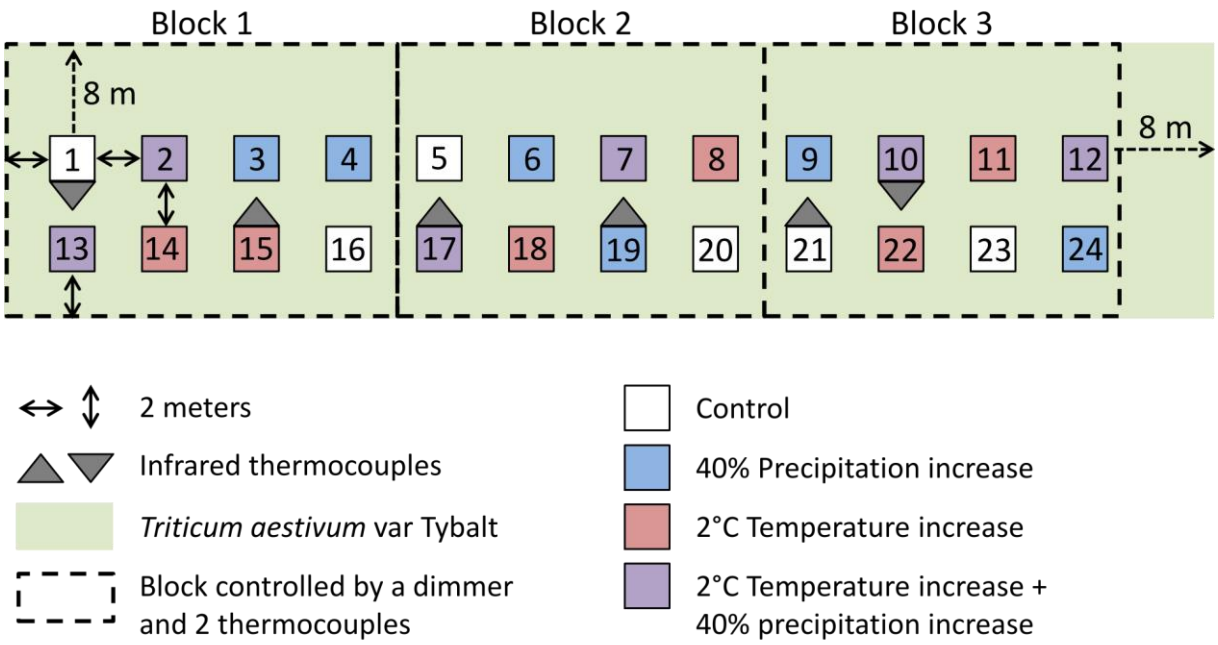
1.5.2 Chapter 3: Simulated Climate-warming Reduces Floral Resources, Altering Insect Visitation and Wildflower Seed Set in a Cereal Agro-ecosystem

In Chapter 3, I employed an open-air simulated climate warming experiment to investigate the bottom-up effects of simulated warming on wildflowers and pollinators (see Figure 1.3 below). Situated on an arable farm in North Yorkshire, the fully-replicated experiment had four climate change treatments: 2 °C increase in temperature above ambient ('Heat'); 40% increase in precipitation ('Water'); warming and precipitation treatments combined ('Heat+Water'); and ambient conditions ('Control'). I collected and analysed data on the impacts of the climate change treatments on floral abundance, floral nectar volumes, species richness, insect visitation, and community similarity. I also constructed and analysed replicated plant-pollinator interaction networks to investigate the effects on network structure and complexity. Finally, I examined seed set data to provide an insight into how pollination services were affected by the treatments.

1.5.3 Chapter 4: Unravelling the effects of simulated warming on plant-pollinator interactions within and between years

Chapter 4 represents an application of innovative and novel temporal network analysis techniques to investigate how the effects of climate change upon plant-pollinator communities vary through time. There is growing evidence indicating that the temporal dynamics of species interactions are an important, but overlooked, aspect of network ecology. Given the highly seasonal nature of the UK's climate and wildlife, and the potential importance of phenological advancement, it is crucial to investigate the temporal aspect to any climate change impacts. All the data for this chapter came from the same experiment as that of Chapter 3, but instead of it being aggregated over time, the dataset was expanded. This allowed me to investigate both the temporal dynamics of, and treatments effects upon, floral abundance, insect community composition, interaction frequency, and species and interaction turnover.

a)



b)

Figure 1.3 Simulated warming experiment; a) experimental design; b) photograph of the site in July 2014

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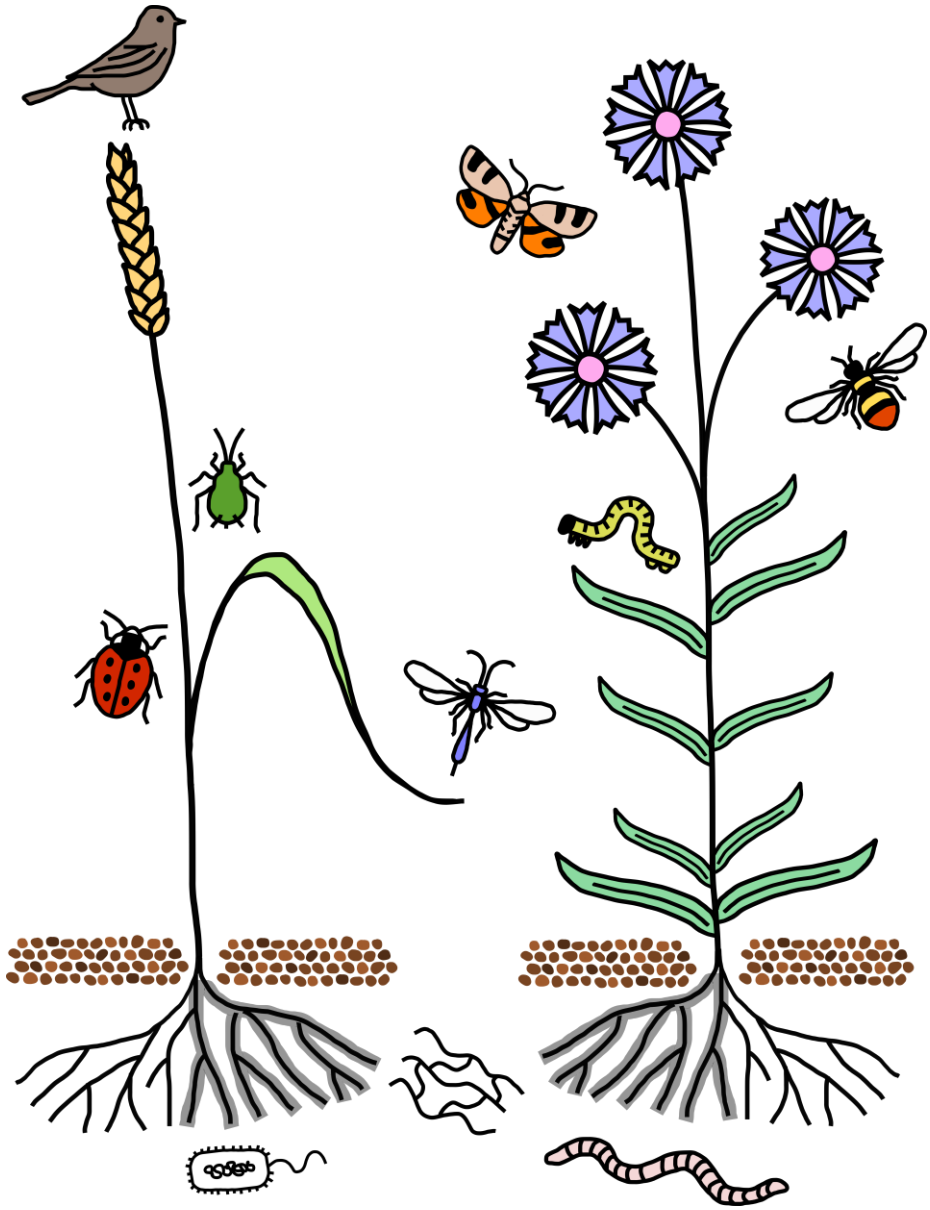
Chapter 2: Investigating the impacts of climate change on ecosystem services generated by biodiversity in agro-ecosystems: an application of the DPSIR framework



Abstract

Understanding and predicting how climate change will affect agro-ecosystems and the ecosystem services they provide is a significant global challenge. Investigating this topic requires a holistic approach that can capture the complexity of agro-ecosystems and the impacts of climate change upon their physical, biological and socio-economic aspects. The DPSIR framework is a problem structuring method that can be used to collate and synthesise multi-disciplinary evidence from a wide range of sources. Here, we create a DPSIR framework that characterises the impacts of climate change on some key ecosystem services directly generated by farmland biodiversity, using UK agriculture as a case study. Initial structuring of the framework was hindered by inconsistent approaches in the literature regarding the definitions and classifications of ecosystem services and the DPSIR categories. We found the standard DPSIR framework to be suitable for modelling UK agro-ecosystems at a broad scale, but it lacked the fine-scale detail and specificity that are necessary if the full scope of the system and the climate change impacts are to be characterised. Therefore, we developed a novel three-step methodology, which involved two separate iterations of the initial DPSIR framework (the first-step), each with a distinct and narrower focus. The second-step of the method allowed exploration of the detailed cause and effect relationships for the selected organism groups (pollinators, pest regulators and arbuscular mycorrhizal fungi) by focusing on a subset of the elements within the first-step; this highlighted knowledge gaps within the literature concerning the impacts of climate change on species interactions and community structure and any cascading impacts on ecosystem services. Cultural services were also highlighted as an area where further research is needed to establish how biodiversity loss may affect their delivery. The third-step of the method involved temporally restricting the framework to the present dominant understandings within the current literature, allowing the expected climate change responses of the different features of agro-ecosystems to be summarised and displayed; this demonstrated striking negative impacts on biodiversity, soil quality, crop yields and a wide variety of ecosystem services and goods. The novel three-step DPSIR approach developed here would be useful for modelling other large and complex systems where detail and directions of change are necessary.

2.1 Introduction

By the end of the 21st century, and relative to records for the period 1850-1900, global surface temperature change is likely to exceed 1.5 °C, precipitation patterns will be significantly altered, extreme weather events will increase in severity and frequency, and atmospheric CO_2 concentration is predicted to increase (IPCC, 2013). These changes are expected to negatively affect crop yields (Asseng et al., 2015; Long et al., 2006; Parry et al., 2004), which has major implications for global food security, particularly given the rapidly growing global human population (IPCC, 2014a). Global climate changes are also expected to impact biodiversity significantly (MEA, 2005), indeed, there is a strong body of evidence showing that recent climatic changes have already affected many species including pollinating insects (Kerr et al., 2015; Parmesan and Yohe, 2003); this loss of biodiversity could affect ecological processes such as pollination, which will further impact food production (MEA, 2005; UK NEA, 2011a). Finding ways of managing agro-ecosystems to minimise the adverse impacts of climate change on both the crop and non-crop biodiversity within them, is therefore a significant global challenge. However, management of agro-ecosystems can be very problematic due to the complex interplay between the various natural, social, and economic components; to effectively manage such systems requires a holistic approach that can capture the divergent interests of all relevant stakeholders and the complexity of the system's structure, processes, and impacts. One such approach is the Drivers – Pressures – State changes – Impacts – Responses (DPSIR) framework; it is a problem structuring method that serves to capture and represent the causes, consequences and responses to change in a systemic way (Gregory et al, 2013). Here, we use the DPSIR framework to investigate how climate change might affect the delivery of ecosystem services within agro-ecosystems, with a focus on the regulating services provided by biodiversity.

Global food security is an issue that is gaining momentum in the public and political arenas, and so the question of how to feed a growing human population without destroying biodiversity is increasingly being recognised as a significant challenge (Godfray et al., 2010; Tscharntke et al., 2012). This is further complicated by the uncertainties and problems that climate change will bring (IPCC, 2014a; Knox et al., 2012). For example, climate change is expected to increase crop yield in temperate developed countries due to the increased availability of atmospheric CO_2 for photosynthesis, while tropical and sub-tropical

developing countries are expected to experience declines in yield due to reduced precipitation and increased temperature (Parry et al., 2004). This may put pressure on developed nations to further intensify agricultural production to make up for short-falls elsewhere in the world. However, an increasing body of evidence indicates that crop yields will decrease in temperate developed countries as a result of temperature increases (Asseng et al., 2015; Liu et al., 2016), and it is likely that the yield increases caused by raised CO_2 will not be sufficient to offset the losses due to raised temperature (Batts et al., 1997; Cai et al., 2015; Guoju et al., 2005; Long et al., 2006). In addition to the effects from constant climatic changes, regional crop yields are also susceptible to unpredictable extreme weather events (Lesk et al., 2016). Recent years have seen examples of significant crop yield decreases as a result of extreme flooding (Chau et al., 2014), heat waves (De Bono et al., 2004), and frosts (Gu et al., 2008). The situation is complicated further because crop yields are not only subject to the direct impacts of climate change upon the crop plants themselves, but also indirect effects via changes to the biodiversity that interact with them; for example, increasing temperatures will lead to an increased abundance and diversity of crop pests and pathogens, which could certainly affect yields (Bebber et al., 2014; Harrington et al., 2007). Nevertheless, it is important to recognise the potential for climatic changes to affect all the non-crop biodiversity within agro-ecosystems, not just the pests, because many organisms perform beneficial functions that can protect and enhance crop yields (MEA, 2005; UK NEA, 2011a, 2011b).

Ecosystem services have been defined in many different ways (Boyd and Banzhaf, 2007; Costanza et al., 1997; Daily, 1997) with one of the most widely cited that of the Millennium Ecosystem Assessment (MEA, 2005): ‘ecosystem services are the benefits provided by ecosystems that contribute to making human life both possible and worth living’. In practice, this means that any normal ecosystem functions or processes that can directly or indirectly benefit humans in some way, can be considered ecosystem services; most of these functions and processes are biological in nature, such as insect pollination and timber growth, while others involve physical and chemical aspects, such as soil formation. Agro-ecosystems provide a range of ecosystem services including those that directly benefit people, such as the provision of food crops, bioenergy, and providing spaces and landscapes offering opportunities for recreation, and others that provide indirect benefits, with soil quality regulation, nutrient cycling and carbon sequestration being three prominent

examples (Power, 2010; UK NEA, 2011c). However, the provision of one service can impact the delivery of others, especially when humans seek to enhance delivery of one or more services with little regard for the others; agricultural intensification in the 20th century led to widespread environmental degradation that included the loss of species and habitats (Robinson and Sutherland, 2002; Stoate et al., 2001) and, in order to meet growing demands for food, further environmental and ecological degradation is highly likely (Tilman et al., 2011). Despite international legal provisions in place to protect endangered species and rare habitats, such as the international RAMSAR wetland convention (*Ramsar Convention*, 1971) and the EU Birds and Habitats Directives (Council of the European Union, 2009, 1992), as well as legislation to protect some other aspects of the natural environment, such as the EU Water Framework Directive (Council of the European Union, 2000), the majority of species and habitats present in agro-ecosystems remain legally unprotected. Degradation and loss of unprotected biodiversity and habitats has consequences for ecosystem service provision (Power, 2010), particularly as many of these services are directly provided by specific organisms (e.g. insect pollinators), which makes biodiversity conservation even more important (Mace et al., 2012). However, the UK National Ecosystem Assessment - which aimed to provide a comprehensive evaluation of the ecosystem services provided by the UK's natural environment - demonstrated significant 'knowledge gaps' and uncertainties relating to the complex interactions between the various organisms and processes responsible for delivering the different services, and the impacts that climate change may have upon them (UK NEA, 2011b, 2011a, 2011d, 2011e).

Given the complexity of agro-ecosystems and the intricate relationships between the diverse range of ecosystem services they provide, investigating the potential impacts that future anthropogenic climate change may have on these systems and services is a significant challenge. It is essential that a holistic approach is employed to assess this topic, one which can bring together information, concerns and issues that stem from agriculture, ecology, socio-economics and policy (Poppy et al., 2014; Robertson and Swinton, 2005; Stoate et al., 2001). The DPSIR framework (Figure 2.1) is a knowledge elicitation and problem structuring approach that is most often employed to support decision making. The structure of the framework necessitates a focus on the assessment, management, and communication of environmental issues, and dictates a clear portrayal of cause and effect relationships (Gregory et al., 2013; Tscherning et al., 2012). Using the DPSIR framework to structure a

problem provides a common framework within which to compile the impacts, requirements, involvement, and/or advice, from the potentially diverse range of sources and contributors involved (Odermatt, 2004). 'Driving forces' (D) refer to social, economic and environmental drivers of change; these are usually the broad-scale features that are ultimately responsible for change, such as climate change and population dynamics (Gabrielsen and Bosch, 2003). 'Pressures' (P) are the specific manifestations of the 'Drivers' upon the system in question; these are the (usually) smaller-scale mechanisms by which change occurs, such as increasing temperature and increased urbanisation. 'State changes' (S) are the observed or predicted changes in the natural environment within the system in question, which occur as a result of the 'Pressures', such as reduced biodiversity and habitat loss. 'Impacts' (I) is where the human and social aspects of the system are characterised; this is where the repercussions of the environmental change upon human welfare are detailed, which could include reduced food production and loss of environments in which people can enjoy nature. 'Responses' (R) are the actions that humans and society put in place in response to the 'Impacts'; these could include both broad- and small-scale measures depending upon the system in question, such as government policies and site management plans (see Figure 2.1). The DPSIR framework is particularly well-suited for consideration of ecosystem services (Atkins et al., 2011a; Gregory et al., 2013; Kelble et al., 2013; Pinto et al., 2013; Rounsevell et al., 2010) and examination of the impacts of contemporary changes in climate (Holman et al., 2008; Omann et al., 2009), because it can capture systemic impacts going beyond natural science.

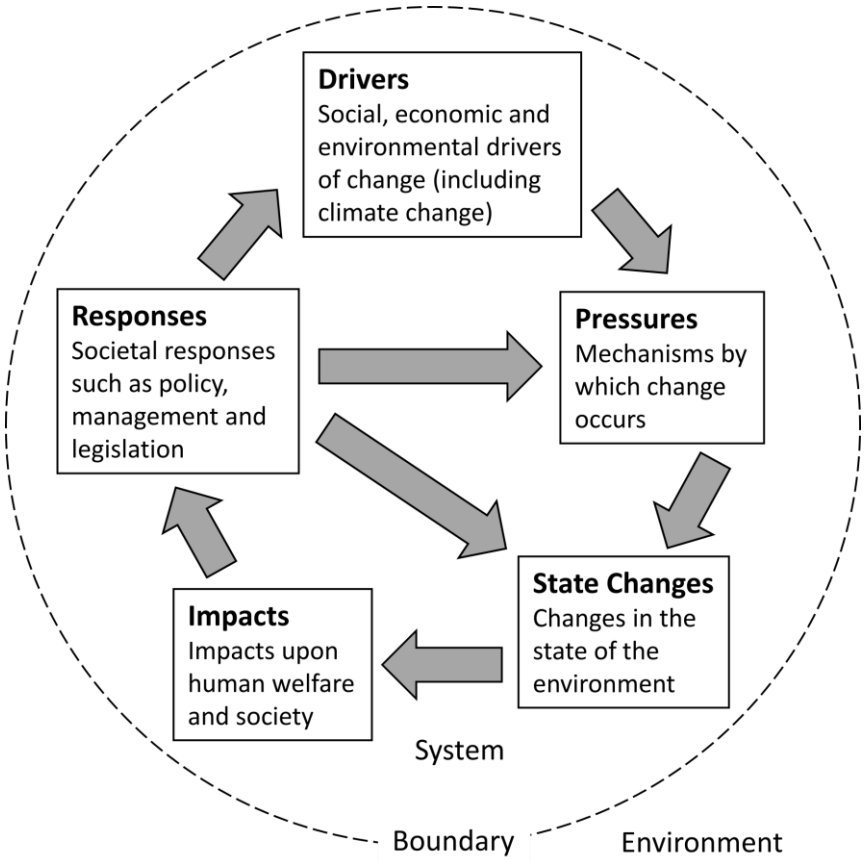


Figure 2.1 The DPSIR framework, showing the cyclical nature and position of the system and boundary within the environment

By examining the impacts of climate change on ecosystem services provided by farmland biodiversity, the objectives of this study are fourfold: (1) to explore the suitability of the DPSIR framework as a tool to combine information from agriculture, socio-economics and ecology to guide investigation of the consequences of climate change on the delivery of ecosystem services provided by biodiversity in agro-ecosystems; (2) to use the DPSIR framework to determine specific relationships, knowledge gaps, and research questions that require further investigation; (3) to use the literature collated in the DPSIR framework to generate an overview of the specific changes to the features in the State changes and Impacts category that can be expected as a result of predicted climatic changes; and (4) to form the basis of an approach that can be developed for other countries, regions and agro-ecosystems.

The DPSIR framework presented in this paper was created using a rigorous, peer-reviewed, and evidence-based methodology as detailed below. We focussed on arable farming in the UK as a case study because it can be considered representative of Northern

Europe and other developed temperate regions in terms of climate and types of farming systems. Moreover, there is a large body of published agro-ecological research conducted in the UK from which we can draw. Consequentially, the central issue that provided a focus and boundary for development of the DPSIR framework in this research, is the impact of climate change on ecosystem services generated by biodiversity, in arable farmland in the UK. However, rather than accounting for all possible organisms that are found in British agro-ecosystems, which would have been too great an undertaking for a single thesis chapter, we instead restricted our investigation to those organism groups that were being investigated experimentally in the Stockbridge Farm simulated warming experiment (Berthe et al., 2015); pollinators (by myself, see the subsequent Chapters 3 and 4), pest regulators (by my colleague Dr Stephane Deroclés, see Deroclés et al. (2018)), and Arbuscular Mycorrhizal Fungi (AMF) (by Dr Darren Evans).

2.2 Methods

2.2.1 Ecosystem services

While the concept of ecosystem services is common to all academic disciplines that employ it, there is a divide between researchers of certain fields in the specific definitions of ecosystem services that they use, and in the understanding of how humans benefit from them (La Notte et al., 2017). Generally speaking, in natural science fields the understanding is holistic and bio-centred: each ecosystem service is itself a beneficial process, so crop pollination benefits us by providing and/or increasing crop yields (IPBES, 2017; La Notte et al., 2017; MEA, 2005; UK NEA, 2011a); while researchers in economic fields take a more reductionist and human-centred view: each ecosystem service is not itself a benefit, but a link between an ecosystem and a potential good/benefit, and that some form of 'capital' is required for humans to receive the good/benefit, so crop pollination increases crop yields, but the crop has to be harvested and processed before humans can receive the goods (Atkins et al., 2011a; Elliott et al., 2017; Fisher et al., 2009; La Notte et al., 2017). These two different viewpoints have also given rise to different classification systems for ecosystem services. Natural and environmental sciences research usually employs the holistic classification system used in the MEA: supporting services underpin all other services by providing physical structure, creating niches and by capturing and converting energy; regulating services contribute towards a function or provision or regulate a specific

ecosystem process that also benefits society; provisioning services directly result in goods/benefits; and cultural services comprise all the educational, spiritual, emotional, aesthetic, cognitive and health and well-being benefits that people receive from interacting with and/or experiencing nature (MEA, 2005). Socio-economic and policy research more often employs a more reductionist classification system: intermediate services are those whose ecological processes and functions support all life and all other services; and final ecosystem services are the outcomes from ecosystems that directly lead to good(s) that are valued by people (UK NEA, 2011f). It is important to note that the position of a service can be dependent on the system in question; in certain contexts, some services may be considered intermediate, while in others they would be classed as final (UK NEA, 2011f). This context-dependant classification of services is particularly relevant here, given that it could affect the placement of elements within the DPSIR framework. A relevant example of a service that fits into multiple categories is wild species diversity, which could be classed as intermediate when considering the potential for wild crop plant relatives to support future crop production, or it could also be classed as final when considering the cultural services and benefits that wild plants and animals provide. Another example is pest regulation, which could be classed as intermediate when considering the potential impact on crop plant disease regulation, or it could be classed as final when considering the direct impact on crop yields.

Because the DPSIR framework developed in this study incorporates evidence from multiple fields including biology, socio-economics and policy, it is important that the definitions and classifications employed here can incorporate both reductionist and holistic views into the structure of the framework. Several classification systems were examined with respect to the specific needs of this research. The Common International Classification of Ecosystem Services (CICES) (Haines-Young and Potschin, 2018) provides a very thorough and holistic classification of ecosystem services, and while it does include a goods/benefits category, it does not classify services as intermediate or final and so would not integrate as well with the reductionist view-points and classifications found in socio-economic literature; as a result it also fails to account for the potential for a given service to straddle the two categories in different contexts. The cascade model (Potschin and Haines-Young, 2011) takes a broader and less detailed view, focusing on the wider context of ecosystem services, but it does not actually distinguish between different types of service. The UK National Ecosystem

Assessment Technical Report (UK NEA, 2011f) included a hybrid system that classified all services according to both a holistic and reductionist method, which also incorporated the potential for services to be both intermediate and final; this method was therefore deemed to be the most appropriate for this research. By expanding on the UK NEA hybrid system, we created an ecosystem service framework (Figure 2.2) that was able to: integrate with the different classification systems employed by the evidence collected during the literature search; integrate well with the structure of the DPSIR framework; and reduce the likelihood of errors relating to double-counting, omitting, or misplacement of elements within the DPSIR framework.

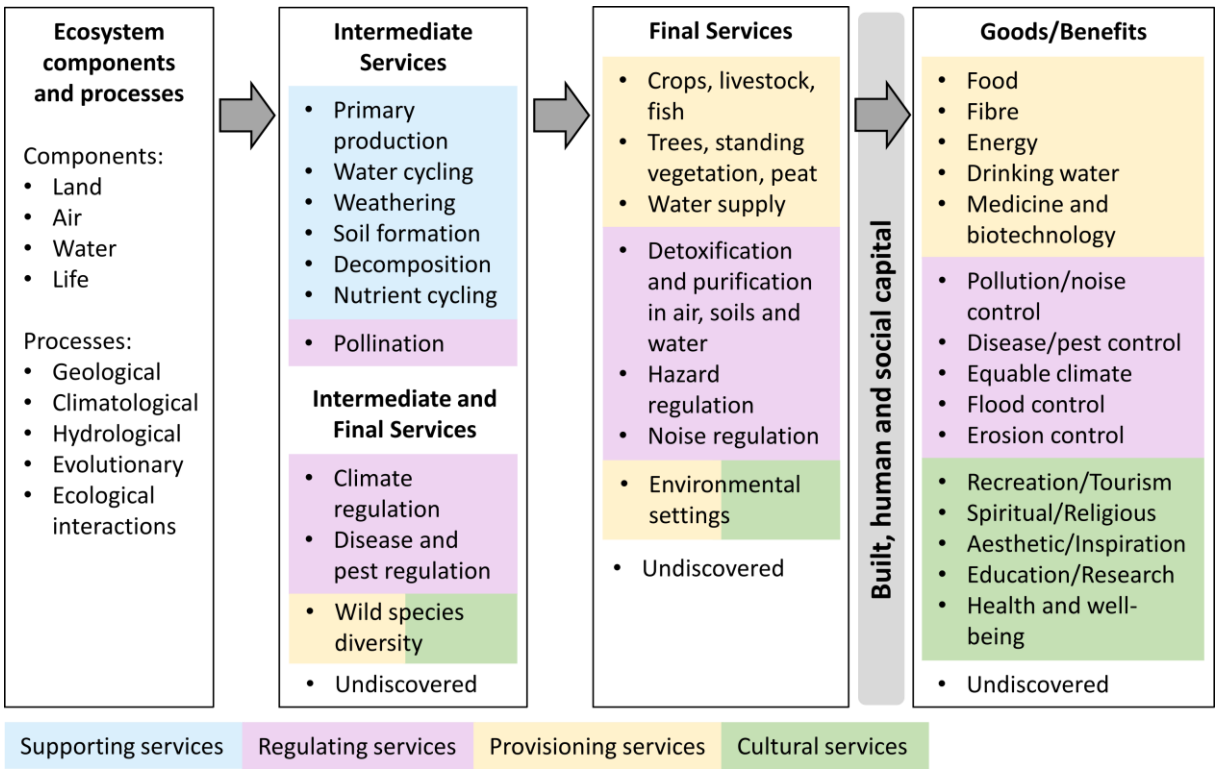


Figure 2.2 The Ecosystem Service Framework: ecosystem processes, intermediate and final ecosystem services, and goods/benefits used in the UK NEA (adapted from Figure 2.3, UK National Ecosystem Assessment Technical Report).

Given the objectives of this study, and that many ecosystem services are delivered, at least in part, by a large and complicated community of interacting species, this research will place specific focus on the services provided by three of the most important groups of organisms in UK agro-ecosystems. These groups of organisms are: (i) pollinators – 35% of global crop production volume is dependent on animal pollinators and 87 of the most

important global food crops are reliant upon them (IPBES, 2017; Klein et al., 2007); (ii) pest regulators – these organisms play a pivotal role in supressing pest populations, which results in reduced crop damage, improved yields and could reduce the need for insecticide use (Cardinale et al., 2003; Östman et al., 2003; Whelan et al., 2008); and (iii) arbuscular mycorrhizal fungi (AMF) – these are symbiotic fungi that colonise the roots of around 80 percent of all plant species and contribute to at least six different ecosystem services in agro-ecosystems: soil stability, nutrient uptake, tolerance of abiotic stressors such as drought, tolerance of biotic stressors such as herbivorous insects, resistance to soil pathogens, and crop nutrition (Gianinazzi et al., 2010; Gosling et al., 2006; Smith and Read, 2008). All of these above- and below-ground interactions can occur simultaneously within agro-ecosystems and are susceptible to the effects of climate change.

2.2.2 DPSIR Framework

Our use of the DPSIR framework is due to its properties as outlined in the introduction (2.1, but also 1.4 in Chapter 1), including its capacity to combine information from a range of sources and capture human and environmental interactions (Gabrielsen and Bosch, 2003; Gregory et al., 2013). The evidence base from which the DPSIR framework can be populated comprises one or more interdisciplinary, multidisciplinary or transdisciplinary methods: literature searches, direct input from the research team, stakeholder engagement, and consultation of relevant legislation (Tscherning et al., 2012). To construct the DPSIR framework in this study, a literature search approach was employed involving two academic search tools, Web of Science (http://wok.mimas.ac.uk/) and Google Scholar (https://scholar.google.co.uk/), and search terms based on Drivers such as “climate change/warming” in combination with the other features, e.g. “pollinat*”, “ecosystem services”, “food security”, and “biodiversity”. Non-academic literature was researched using the standard Google search engine (https://www.google.co.uk/) and the UK Government publication repository (https://www.gov.uk/government/publications). Reference material used included: academic journal articles and research monographs, UK and EU policy documents, government department research publications, intergovernmental research reports, and the documents of the UK National Ecosystem Assessments. Given we searched for the seminal and the most relevant documented evidence for the area of enquiry, the list of references identified in this paper is not meant to be exhaustive of all evidence supporting

the various relationships depicted by the DPSIR framework. Adopting this rigorous and objective evidence-based approach enables us to identify knowledge gaps within the published scientific literature and assemble expectations of the specific changes agro-ecosystems can expect as a result of climate change. While it is generally agreed that the inclusion of stakeholders in the construction of the DPSIR framework can result in a more relevant, complete, and useful model (Svarstad et al., 2008; Tscherning et al., 2012), particularly if it is to be used to support specific management or policy measures, stakeholder engagement was considered unnecessary for this study, given the more limited research objectives. Stakeholder engagement was also deemed to be beyond the project budget, particularly as the DPSIR research constitutes only one chapter of a larger thesis. Nevertheless, there are many studies that have produced and successfully employed a DPSIR created using only a literature review approach (Tscherning et al., 2012).

The DPSIR framework is a systems-based method, which means that clarity over the boundary of the system in question is vital (Atkins et al., 2011b). The scale of the system is an important consideration in defining its boundary, and this obviously relates to the issue or research question under investigation. In general, establishing the boundary might refer to: a relevant decision-making unit, such as a nature reserve or local authority boundary; a spatial dimension if the application is to a specific geographical area, such as a river catchment or mountain range; a temporal dimension if the issue relates to particular events, such as a natural disaster or land use change; or a combination of factors. The boundary will determine which Pressures and State changes are included in the DPSIR, though Drivers, Impacts and Responses could extend beyond the boundary as they may operate on different scales (Svarstad et al., 2008). To be consistent with the objectives of this study, the boundary was determined to be UK arable agro-ecosystems, and the ecosystem services provided by biodiversity in those systems. The temporal scale of the initial DPSIR framework created here was unbounded, which means that the elements within the framework are characterised in a neutral fashion rather than indicating an expected or current change; for example, the Pressures are all described as “changes in” rather than “increases/decreases in”. This distinction has two main benefits: the structure of the framework is relevant beyond the current dominant understandings and predictions within the literature, which may change over time with further research, and it avoids over complication of the framework’s depiction.

It is essential to clearly define the different the DPSIR categories for the system as well as its boundary:

- **Drivers** are defined here to be both anthropogenic and environmental, and so includes climate change. Treating climate change as a Driver is consistent with other research that has focussed on climate change (Bär et al., 2015; Holman et al., 2005a, 2005b) and ecosystem services (Kelble et al., 2013; Rounsevell et al., 2010), and the position of the MEA (2005), NEA (2011b, 2011a, 2011d) and the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES, 2017). However, it is acknowledged that climate change can be considered a Pressure, or more specifically an unmanaged pressure exogenic to the system (see Elliott et al., 2017).
- **Pressures** are imposed upon the system by the Drivers and includes the specific climatic changes that are expected within the UK, such as changes in precipitation and temperature.
- **State changes** include the biotic and abiotic changes in the natural environment that result from climate change and, as such, include relevant supporting and regulating ecosystem services as these constitute aspects of the physical, chemical and biological environment.
- **Impacts** refers to changes in human welfare that follow-on from the changes in the State of the natural environment and associated ecosystem services, as these affect goods/benefits. For example, impacts include the effects of changes to provisioning and cultural ecosystem services as these can have quite tangible, societal welfare consequences (Atkins et al., 2011a; Gregory et al., 2013).
- **Responses** represent the relevant policy and management strategies that feedback within the system to influence the Drivers, Pressures and State changes.

2.2.3 Three-step process

The agro-ecosystem was investigated here at a broad-scale to allow us to explore the environmental and societal repercussions of climate change in a comprehensive way and address this study's first research objective of combining information from a variety of disciplines and sources to explore the effects of climate change. However, to address the

second research objective, of identifying knowledge gaps and specific relationships that require further investigation, a more detailed examination was required. Therefore, an additional process was employed that operated at a smaller scale, effectively focussing on some of the key causal relationships within the DPSIR framework that relate to the three focal organism groups (pollinators, pest regulators and AMF). The third objective, of providing predictions of how climate change will affect the elements within the State changes and Impacts categories, also required a separate method. To meet this final objective it was necessary to restrict the temporal scale to examining changes that are expected to occur by the end of the 21st century (relative to records between 1850-1900) under current climate projections of global surface temperature change exceeding 1.5 °C, precipitation patterns altering, extreme weather events increasing in severity and frequency, and atmospheric CO_2 concentration increasing (IPCC, 2013).

Consequently, the results associated with the DPSIR framework for temperate arable farming agro-ecosystems are presented in three stages:

1. A DPSIR framework that describes how climate change and other relevant Drivers will affect agro-ecosystem biodiversity and the ecosystem services it provides;
2. A more detailed and focussed iteration of the initial DPSIR framework that elaborates on some of the key relationships to more clearly and completely show the cause and effect pathways and any knowledge gaps;
3. A more temporally relevant and specific iteration of the initial DPSIR framework that shows the directions of change for each of the Pressures, State Changes and Impacts, based upon current evidence of what is expected to happen under current climate projections for the rest of this century.

Steps 2 and 3 of this method involve making judgements with respect to the strength of the literature supporting the causal links and directions of change. Such strength of evidence was determined by a combination of factors, similar to the methods adopted by Hooper et al. (2017): the volume of research supporting the link, the relevance of the research, the strength and nature of the link identified, and the degree of agreement between studies on the nature and strength of the link. Table 2.1 outlines the specific

evidence strength categories and the symbols that denote them within the figures for steps 2 and 3.

Evidence Strength	Causal Relationship	Step 2 Symbol	Step 3 Symbol
Multiple relevant papers showing direct links AND Little disagreement on the nature/strength of the link	Stated		
Only 1 or 2 relevant papers showing direct links OR Contradictory evidence on the nature/strength of the link OR Published evidence did not relate to the system in question	Inferred		
No relevant papers showing direct links BUT Biologically rational	Potential		?

Table 2.1 Evidence strength categories and their corresponding symbols used to carry out steps 2 and 3 of the DPSIR analysis. The step 2 symbols are used in Figures 2.4-2.6 and the step 3 symbols are used in Figure 2.7.

2.3 Results

The literature search resulted in a collection of over 80 seminal or key papers, reports and policy documents that were selected to provide support for inclusion of the various elements within the DPSIR framework; these references are denoted within all the figures in this chapter by a number, a list of these references and their corresponding numbers can be found in Table 2.S1 in appendix 2.6. In some cases, only one or two references may accompany a feature within the DPSIR; this is either due to there only being that number of relevant references, or no others were required as those references are comprehensive and recent literature reviews.

2.3.1 Step 1: DPSIR for UK agro-ecosystems

Figure 2.3 depicts the DPSIR framework created to collate and display the main effects of climate change on UK agro-ecosystems. It identifies significant aspects of the system and while we aimed for it to be comprehensive, we recognise that there is potential

for additional elements to be included. Although the main Driver was always going to be climate change given the aims of this study, it became necessary to include two other Drivers (human population, and food preferences and markets) due to the inseparable nature of the agro-ecosystem's features and its function (Figure 2.3). The Pressures follow logically from the Drivers and include the context specific mechanisms by which those drivers stress the system; this includes specific climatic changes and agricultural management practices. The State changes includes all the environmental changes that arable agro-ecosystems experience as a result of at least one of the Pressures; changes in these elements inevitably affects their related ecosystem services, which is demonstrated by the coloured boxes beneath them. Most of the ecosystem services shown as State changes are regulating services driven by the system's physical and biological features and can therefore be considered intermediate and/or final services, but others including the provisioning service of crop production (a final service), and the supporting service of nutrient cycling (an intermediate service) are also present. Impacts includes all the specific ways that people in the UK are affected by the State changes and are all displayed as ecosystem services, though they can also be considered as goods/benefits. Most of the ecosystem services shown as Impacts are cultural and stem from the system's wild species diversity and environmental settings, while the few regulating services originate from its physical features, and the food provisioning service has links to the physical, biological and economic features of the system. The Responses includes many high-level policy directives put in place by the European Union and UK government to protect and maintain agricultural production, biodiversity and habitats, and water quality; all of these policies make specific mention of climate change as a threat and outline specific adaptation and/or mitigation measures and strategies. Indeed, Several UK environmental policy documents include stated commitments to increase the resilience of both natural and agricultural environments, restore biodiversity, prevent soil erosion, improve water and soil management, and improve habitat condition and connectivity (DEFRA, 2018a; UK Government, 2018). Most of the policy documents included in Responses take a reactive rather than proactive approach with respect to climate change; they feedback to directly address negative consequences on the environment (i.e. State changes), rather than minimising or preventing negative consequences by addressing the Pressures, although there is one policy document that attempts to address a Driver (climate change) directly (The Committee on Climate Change, 2013). Responses also includes elements that reflect the smaller scale decisions taken at the

level of the farm business unit; this includes management decisions relating to crop varieties, irrigation, pesticide use etc, but also joining/withdrawing from agri-environment schemes that prescribe a range of wildlife-friendly farming practices such as hedgerow improvement, reducing agricultural water pollution, or creating flower strips for wild pollinators. These farm-level management decisions are also predominantly aimed at directly addressing the State changes, but there is also consideration for the Pressures relating to agricultural management practices.

It is important to note that the elements within the Responses category reflect the relevant legislation and policies in place at the time of conducting this research, which should continue to be the case until at least the 29th of March 2019, when the UK is expected to leave the European Union. While the UK Government has produced some documentation regarding post-exit agricultural policy (DEFRA, 2018b), there is still a great deal of uncertainty with respect to what form of exit will occur (or even if it will), which means that it is extremely difficult to know what new policies will replace those currently stemming from the EU; particularly given the devolved nature of the UK government. As a result of this uncertainty and the unstable political climate, it was decided to only portray those policies firmly in place at the time of writing (2018).

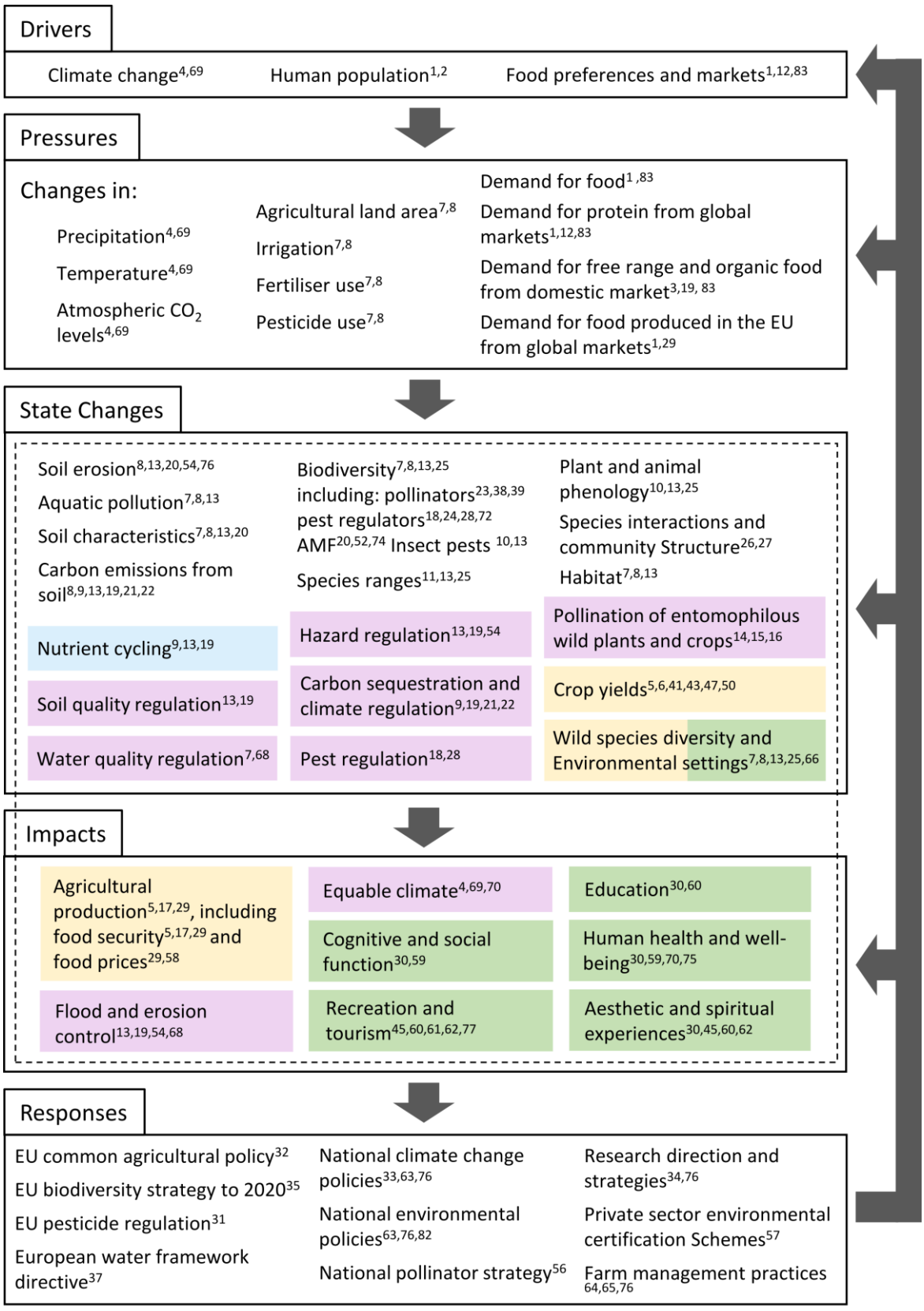


Figure 2.3 DPSIR framework created for UK arable agro-ecosystems. For references, see Table 2.S1 in appendix 2.6.

2.3.2 Step 2: Pathways and knowledge gaps

Here we focus on some of the relationships in the DPSIR framework, concentrating on the three focal organism groups (pollinators, pest regulators and AMF) and the services they provide; this enables us to highlight areas where the evidence is strong and areas where further research may be required. While the previous structure of the DPSIR framework is maintained, it is presented here at a finer scale to permit the more complicated multiple-step cause and effect pathways to be shown diagrammatically. However, even at this smaller scale it would be too problematic to present comprehensive diagrams that incorporate all the relationships between all the relevant elements, and include appropriate annotations, while remaining easy to interpret. To this end, only one climate change Pressure is included in this step: temperature change. While it is recognised that precipitation and CO_2 levels are important environmental factors to insects, birds and fungi, temperature is arguably more important in the context of expected climatic changes in the UK and Northern Europe over the next century (see IPCC, 2013), and in terms of how phenology, range, abundance and other characteristics of the organisms will be affected (Parmesan, 2006). Given that current climate projections indicate that surface temperatures are going to rise (IPCC, 2013; Murphy et al., 2009), almost all temperature related climate change research investigates increases in temperature rather than decreases in temperature - this was certainly the case for all of the evidence collected for specifying the DPSIR in this study. Therefore, this second step of the analysis reflects the literature and defines the Pressure specifically as an increase in temperature rather than as a non-specific change. It is also worth noting that there is an apparent tendency in the literature towards investigations of changes in temperature over other climatic variables for all three groups of organisms, which means there are knowledge gaps with regard to how these organisms respond to changes in precipitation and CO_2 levels, and to combinations of changes in the three climatic factors.

The results for the three focal organism groups are presented separately in Figures 2.4, 2.5, and 2.6, and in Figure 2.S1 (in appendix 2.6), where the three focal groups are combined. In each figure there are several cases where multiple services have been combined into one box, this is done where the references for those services are the same due to their close links and/or where there is strong evidence of direct ecological

connection. Services are not combined where the evidence is weaker, which allows the knowledge gaps to be highlighted more clearly. The pathways from the Pressure to the Impacts are shown relatively linearly, which provides a clear and intelligible structure and again allows the most important knowledge gaps to be highlighted; however, the reality is that there are interlinkages between some of these pathways, particularly in the case of AMF due to the number of linked services to which it contributes.

Pollinators

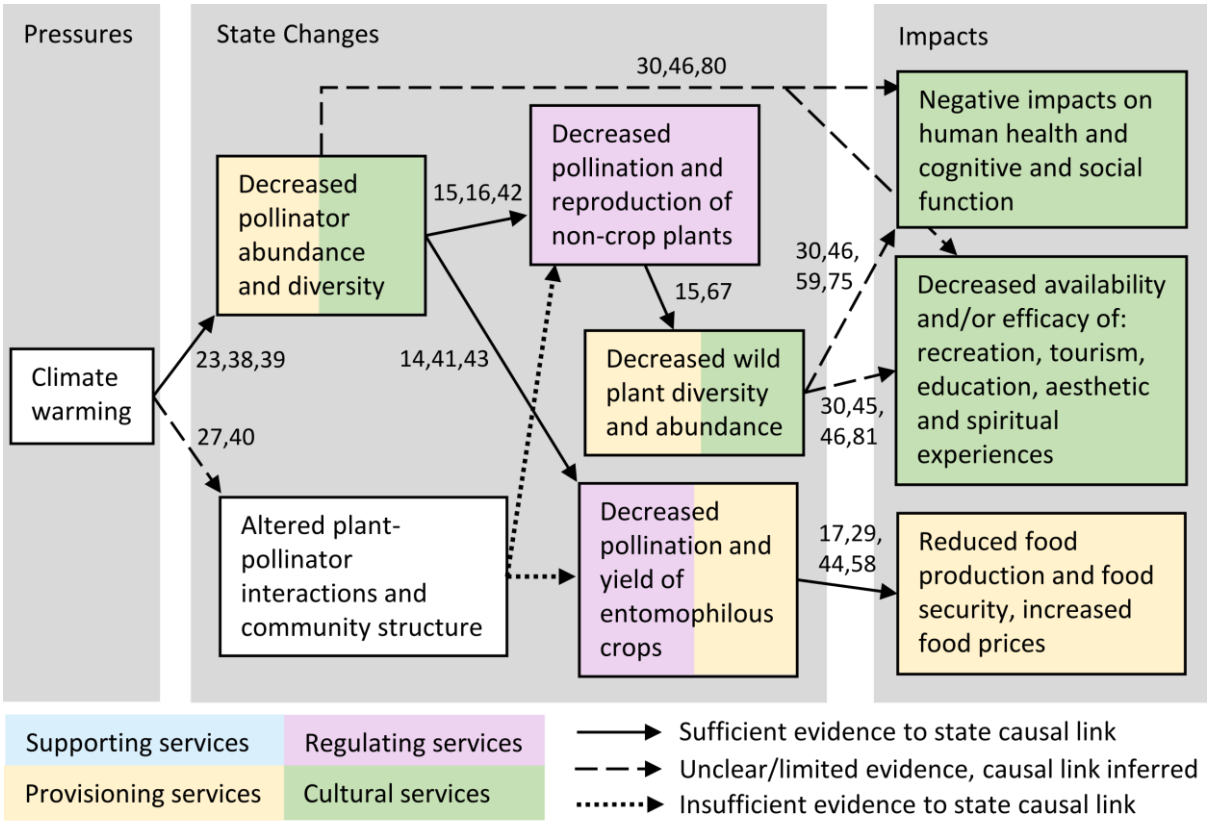


Figure 2.4 A detailed examination of how climate warming impacts the ecosystem services provided by pollinating insects. For explanation of evidence strength, see Table 2.1 in the Methods section 2.2.3. For references, see Table 2.S1 in appendix 2.6.

Declines in pollinator species diversity and abundance have been well documented in recent years (Biesmeijer et al., 2006; Cameron et al., 2011; Fox, 2013; Potts et al., 2010a, 2010b). This decline is attributed to several factors including habitat loss and disease. Climate warming is expected to exacerbate current declines in diversity and abundance in a number of ways and there is already evidence implicating it (see the solid arrow in Figure

2.4). Increasing temperatures cause range shifts in pollinators and plants, but habitat fragmentation and dispersal limitations may prevent species from tracking changes in climate (Kerr et al., 2015; Parmesan and Yohe, 2003). Because specialist pollinators are less likely to be able to shift their range, they are at risk of being replaced in communities and ecosystems by more common generalist species, and losing specialists could have detrimental impacts on pollination services (Burkle et al., 2013; Tscharntke et al., 2005). Flowering times of plants in the UK have been shown to advance in response to climate warming (Fitter and Fitter, 2002) and equivalent phenological advancements have also been documented for some pollinator species (Hassall et al., 2017; Hegland et al., 2009); this advancement can result in phenological mismatching between species of plant and pollinator that are reliant on one another, which can cause severe fitness losses in some species of solitary bee (Schenk et al., 2018) and have detrimental impacts on pollination for some wild plant species (Kudo and Ida, 2013; Thomson, 2010), although not all studies find evidence of such phenological mismatching (Bartomeus et al., 2011; Rafferty and Ives, 2011). The impacts of climate warming on plant-pollinator interactions at the community scale are less clear (hence the dashed arrow in Figure 2.4). Hegland et al. (2009) reviewed literature on phenological changes and concluded that the structure of plant-pollinator networks are likely to be robust to climate change. More recently, Burkle et al. (2013) examined historic datasets for changes in plant-pollinator interactions over a 120 year period, on a site that experienced climatic and land use changes, and found network structure was degraded by spatial and phenological mismatching and species loss; they also found evidence suggesting that this caused a reduction in pollination, but it is unclear how much this is attributable to climate change. There is good evidence linking insect pollinator abundance and diversity to pollination of both crop and non-crop plants, with resultant impacts in crop yields and wild plant abundance and diversity (see the solid arrows in the State Changes of Figure 2.4).

Pollinating insects are a well-studied group of animals, with a wealth of existing studies covering a wide range of species, environments and food plants. However, the literature search identified some knowledge gaps surrounding species interactions and cultural services. There is uncertainty surrounding what effect(s) climate change will have on plant-pollinator interactions and community structure as there are currently very few published papers and these use observational data, simulations, or proxies (see the dashed arrow in Figure 2.4). There is also great uncertainty regarding how any changes in plant-

pollinator interactions at the community scale may affect pollination of wild plants or crops (hence the dotted arrows depicted in Figure 2.4); the link between flower visits (interaction frequency) and pollination has been demonstrated (Kaiser-Bunbury et al., 2017), but there is currently no published research that has linked interaction network structure or complexity to pollination and seed set. Another area that was identified as lacking research focus is that of non-bee pollinators; it has recently become more widely recognised that other insect groups such as hoverflies, wasps and moths can be important pollinators, but that the majority of the literature is concerned only with bees (Senapathi et al., 2017).

Cultural ecosystem services are difficult to quantify and measure due to their complicated, variable, and context-specific nature (MEA, 2005); this has meant that, until recently, little research focus has been placed on these services, and there are currently no published studies that have looked at the direct impacts of climate change upon their delivery. However, there is a growing body of indirect evidence indicating that losing biodiversity and habitats is likely to have negative impacts on a variety of cultural services (Fuller et al., 2007; Sandifer et al., 2015; Twohig-Bennett and Jones, 2018), allowing us to infer that climate change is likely to result in a reduction of cultural service delivery, since we know it will negatively affect biodiversity and habitats (Brown et al., 2012; Parmesan, 2006). While there is evidence demonstrating positive relationships between plant abundance and diversity to cultural services and nature related benefits, there are currently no studies demonstrating that decreases in plant diversity or abundance in the UK leads to reductions in cultural service availability and delivery (hence the dashed lines in Figures 2.4, 2.5 and 2.6). At present, the evidence base is even poorer for pollinators as there are no published studies demonstrating a specific link between the abundance and diversity of pollinating insects and cultural service provision, which means that currently we must rely on the evidence for biodiversity more generally (hence the dashed arrows in Figure 2.4). Given the charismatic nature and appearance of pollinators like honeybees and bumblebees; their positive and prominent portrayal by the UK media (a search for “pollinators” on the BBC website found over 100 links to relevant content from the past 8 years); the recent rise in bee-keeping (according to the British Beekeepers Association); their popularity with the general public (the buff-tailed bumblebee was voted the UK’s favourite insect in 2015, see https://www.rsb.org.uk/get-involved/biologyweek/favourite-uk-insect-poll); and their importance to human education, recreation, and inspiration (IPBES, 2017), it seems highly

likely that detrimental impacts on pollinator populations will have negative consequences for many cultural services and associated benefits.

Pest regulators

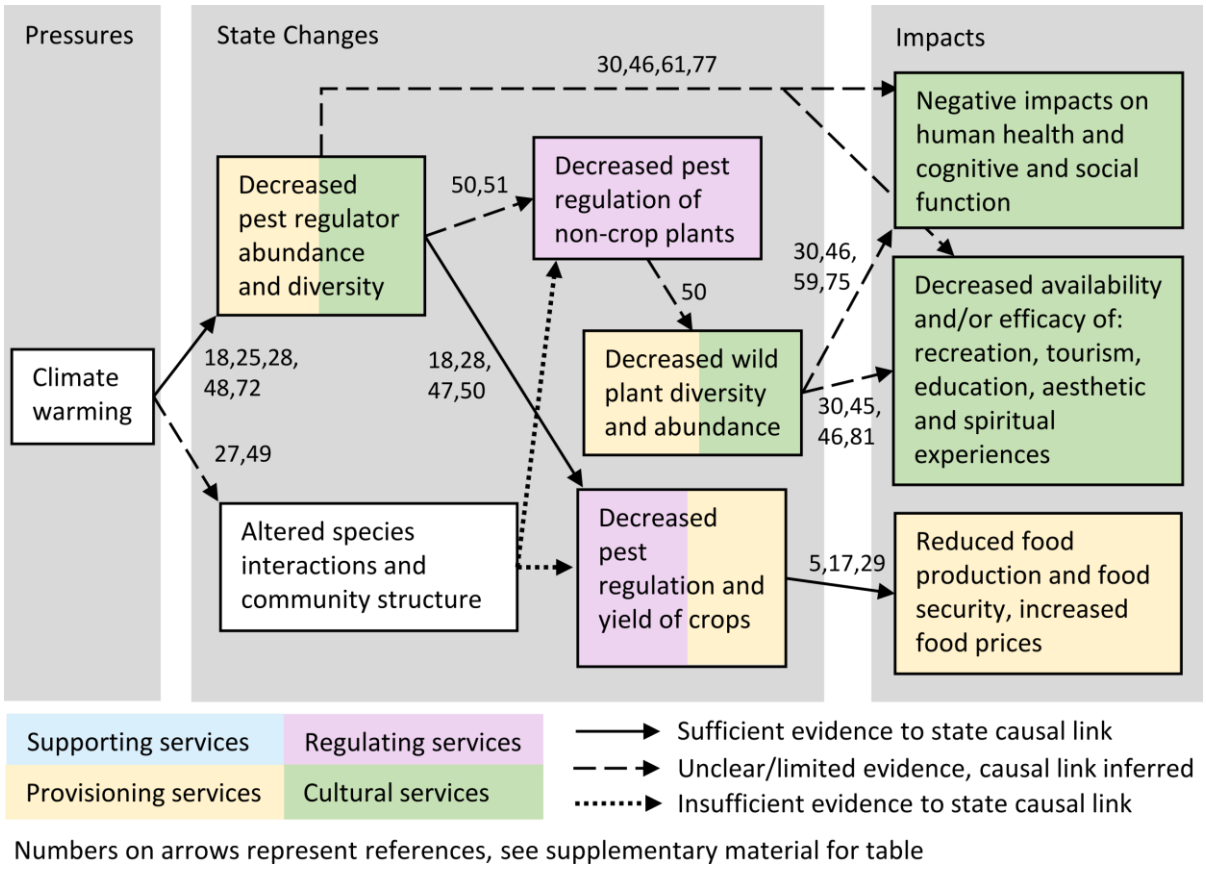


Figure 2.5 A detailed examination of how climate warming impacts the ecosystem services provided by pest regulating animals. For explanation of evidence strength, see Table 2.1 in the Methods section 2.2.3. For references, see Table 2.S1 in appendix 2.6.

Climate warming is expected to affect pest regulating organisms in much the same way that it does pollinators, which is demonstrated by the similarity between Figures 2.4 and 2.5. This similarity between the two groups is unsurprising for two reasons; firstly, the most influential group of insect pollinators in the UK (bees) are closely related to the most influential group of pest regulating insects (parasitoid and predatory wasps); and secondly, many insect species that act as pest regulators due the carnivorous diet of their larval stages, also act as pollinators due to the herbivorous diet of their adult stages. A similar research focus has been afforded to pest regulators as to pollinators, with many studies predicting future changes as well as documenting the impacts that climate change has already had (see

the solid arrow in Figure 2.5). Phenological mismatches between parasitoids/predators and their hosts/prey could affect host/prey availability, offspring survival and parasitism rates (Burgess et al., 2018; Crick, 2004; Jeffs and Lewis, 2013), advancement of bird phenology is well documented and there is some evidence showing it has negative impacts on fitness (Visser et al., 2006). Habitat fragmentation and dispersal limitations may prevent parasites and predators from moving their ranges to track climatic changes (Parmesan and Yohe, 2003). Additionally, climate warming is expected to cause pest numbers to increase earlier in the season and at a greater rate, potentially overwhelming the capacity of natural enemies to control them (Dong et al., 2013; Harrington et al., 2007). The impacts that climate warming will have on host-parasite/prey-predator interactions at the community scale are unclear; several authors have reviewed available evidence but determined that there is insufficient information due to the complexities involved and lack of studies examining this topic (Jeffs and Lewis, 2013; Tylianakis et al., 2008) (see the dashed arrow in Figure 2.5). There is good evidence linking pest regulator abundance and diversity to pest regulation of crop plants, with resultant impacts on crop yields (see the solid arrows in the State Changes of Figure 2.5).

There is a strong body of research covering various aspects of natural pest control by the different animals that provide this service, however, there are several areas that are lacking sufficient evidence. There are many studies that have investigated how pest regulation of crop plants is affected by the abundance and diversity of pest regulators, but very few focused on pest regulation of non-crop plants or what the impacts are for wild plant abundance and diversity (see the dashed arrows in Figure 2.5). Currently there is very little published research that has investigated the impacts of climate warming on pest regulator-pest interactions and community structure; all the available evidence is based on small numbers of interacting species (often just a single pair) and there have so far been no studies that have examined the impacts upon the whole community (see the dashed arrow in Figure 2.5). There is, again, massive uncertainty regarding how any changes in these species interactions at the community scale might affect pest regulation service delivery for both crop and non-crop plants (hence the dotted arrows in Figure 2.5). Another key finding from the literature review was a noticeable focus in the research on parasitoid wasps, while the roles of other animal groups such as birds and other insects are consequently less understood, particularly in the context of climate warming and species interactions.

There is, again, a knowledge gap relating to the delivery of cultural services and goods directly by pest regulating organisms. Therefore, we rely upon the evidence for biodiversity more generally with respect to cultural services, although there is some evidence specifically linking the abundance and diversity of one group of pest regulators (birds) to some cultural services (see the dashed arrows in Figure 2.4). This broad grouping of organisms includes some species that are unlikely to make a large direct contribution towards cultural goods and services due to them being particularly unattractive or uncharismatic, and/or due to the difficulty or low likelihood of observing them as a result of their size, camouflage or inaccessible habitat. Conversely, some predatory insects are popular and likely to be valued by people in much the same way as pollinators (e.g. the seven-spot ladybird was voted the UK's second favourite insect in 2015, and the marmalade hoverfly came in 6th, see https://www.rsb.org.uk/get-involved/biologyweek/favourite-uk-insect-poll). Most ecosystem service research investigating birds tends to focus on the provisioning and regulating services (for example see Whelan et al., 2008), so there is not much scientific evidence linking their abundance and diversity to cultural services and goods. However, given the large memberships of societies like the Royal Society for the Protection of Birds (RSPB) and the British Trust for Ornithology (BTO), the abundance of nature documentaries featuring birds, the high participation in public recording events (see the big garden bird watch, https://ww2.rspb.org.uk/get-involved/activities/birdwatch), and the prevalence and importance of birds in art, literature, music, religion etc., it seems highly likely that detrimental impacts on insectivorous bird populations will have negative consequences for many cultural services and benefits.

Arbuscular mycorrhizal fungi (AMF)

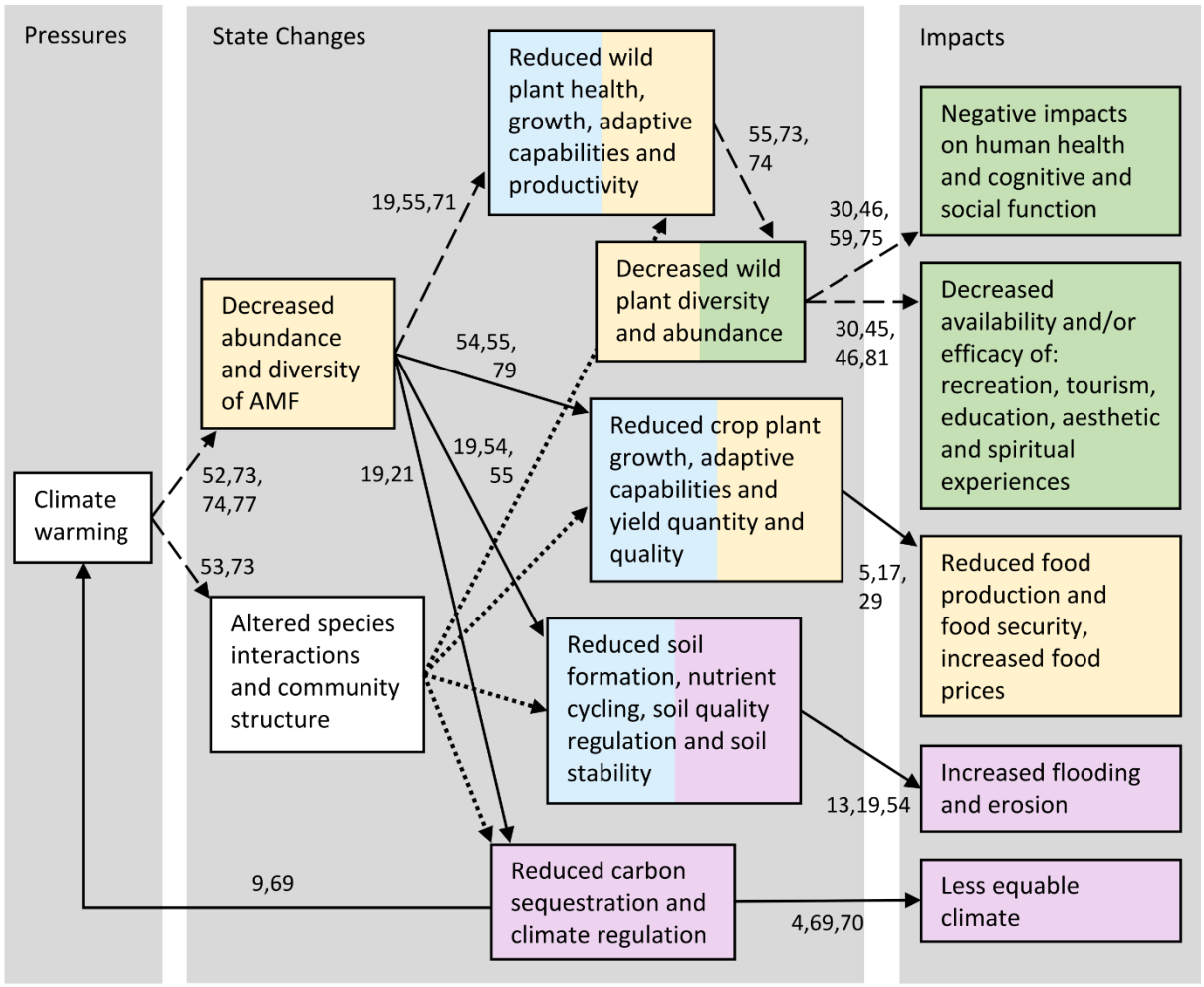


Figure 2.6 A detailed examination of how climate warming impacts the ecosystem services provided by AMF (arbuscular mycorrhizal fungi). For explanation of evidence strength, see Table 2.1 in the Methods section 2.2.3. For references, see Table 2.S1 in appendix 2.6.

Climate warming will undoubtedly affect arbuscular mycorrhizal fungi (AMF) and the services they provide, but due to the complexity of the interactions between the AMF, host plant and abiotic environment, it is extremely difficult to isolate any specific relationships and impacts (Tylianakis et al., 2008) (hence the dashed arrow in Figure 2.6). It is clear that climate warming will lead to altered soil conditions that could change soil communities, structures and interactions, the impacts of which could include: changes in nutrient cycling and nutrient availability, speed of processes like decomposition, extent of carbon release,

and the overall character and fertility of soils (UK NEA, 2011b, 2011a). It is likely that any changes to the biotic and abiotic environment in which the AMF reside, will affect the delivery of the services that AMF provides. There is some evidence that increasing temperature results in a changed AMF community, reduced abundance and diversity of AMF, and that AMF community composition could affect plant community composition the following year (Shi et al., 2017; Sun et al., 2013; Zhang et al., 2016). At the time of writing, there is very little published research on the impacts of climate warming on plant-AMF interactions at the community level (Classen et al., 2015), though it is an area of increasing interest and there is some evidence indicating that elevated temperature leads to reduced AMF root colonisation (Wilson et al., 2016). There is good evidence linking AMF diversity and abundance to a range of ecosystem services relating to soil (formation, quality and stability), nutrient cycling, carbon sequestration and crop plants (growth and yield) (see the solid arrows in the State Changes of Figure 2.6).

AMF are less well-studied than pollinators or pest regulators, and as a result there are more knowledge gaps relating to climate warming and AMF than there were for the other organism groups. Once again there is a lack of focus on the impacts of climate warming on the delivery of services to non-crop plants and any impacts this may have on their diversity and abundance (see the dashed arrows in Figure 2.6). There is a lack of evidence detailing the effects of climate warming on community-scale plant-AMF interactions (see the dashed arrow in Figure 2.6), and massive uncertainty regarding how any such changes may go on to impact AMF service provision (hence the dotted arrows in Figure 2.6). In addition, for AMF there is also insufficient information on how the abundance and diversity of this organism group may be directly affected by climate warming (see the dashed arrow in Figure 2.6). These knowledge gaps are probably due, in part, to the practical difficulties associated with studying these organisms (species identification is extremely challenging), and the difficulty of trying to separate and correctly attribute the physical, chemical and biological processes occurring within soils. The fact that AMF contribute to a relatively large number of ecosystem services also means that there are many more areas to research when compared to other service providing groups like pollinators (Figures 2.4 and 2.6).

2.3.3 Step 3: Directions of changes under projected climate scenarios for the 21st century

In the final step of the analysis, Figure 2.7 reports the expected directions of change in ecosystem services based upon current evidence of how our climate is projected to change, and how these climatic Pressures will affect the State changes and Impacts for arable agro-ecosystems shown in the DPSIR in Figure 2.3. The elements and their positions within Figure 2.3 are retained here in Figure 2.7, the only difference is that the Drivers and Responses have been excluded from this step as they are not necessary in this context. Here, the Pressures have narrowed, when compared to Figure 2.3, to reflect the current predictions of how the climate of the UK (and Northern Europe) will change over the next century (relative to records from 1850-1900). The overwhelming majority of the climate projections and models find the same changes: surface temperature is likely to increase by at least 1.5 °C; precipitation patterns will be significantly altered, in the UK it is likely that overall rainfall will decrease in summer and increase in winter, but the intensity of summer showers is expected to increase; atmospheric CO_2 concentration is predicted to increase; and extreme weather events will increase in severity and frequency (IPCC, 2013; Kendon et al., 2014; Murphy et al., 2009). Figure 2.7 includes arrows that indicate the expected directions of change given the assumptions regarding the changes in the Pressures; these directions of change come from the current dominant understandings in the literature, but the references that provided the necessary evidence (see Figure 2.3 and Table 2.S1 in appendix 2.6) are not displayed here to preserve a clear portrayal and prominent message.

The evidence collected, collated and summarised within Figure 2.7 suggests that almost all of the elements in the State change and Impacts categories will likely experience negative directions of change as a result of climate change. Many of the uncertainties relate to the knowledge gaps discussed previously in Step 2: soil features and related below-ground services, cultural ecosystem services and nature related benefits, and species interactions. As more research is conducted some of these knowledge gaps and uncertainties may be addressed and render Figure 2.7 (and Figures 2.4-2.6) incorrect, but the content of Figure 2.3 and the way that the problem is structured within the DPSIR should remain accurate.

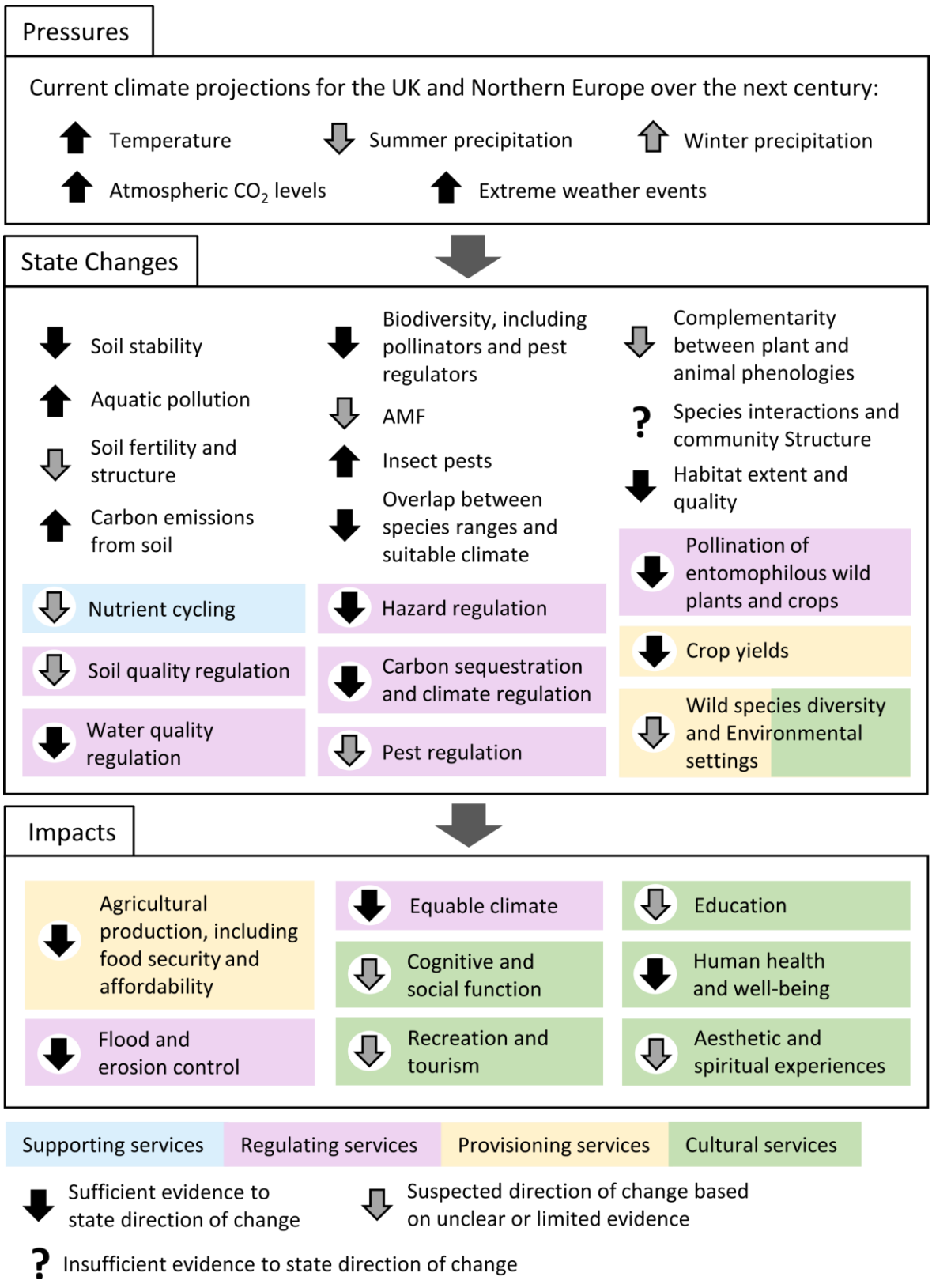


Figure 2.7 Directions of change for the State Changes and Impacts in the DPSIR (Figure 2.3) based on IPCC and Met Office climate change projections, and current dominant understandings in the literature (for references see Figure 2.3 and reference list in Table 2.S1 in appendix 2.6).

2.4 Discussion

We have shown that the DPSIR framework is an effective tool for providing a structure within which to collect and attribute information relating to climate change and agriculture from a range of sources and involving evidence from a number of disciplines. The framework was able to capture the system-wide consequences of climate change and display the pathways between the abiotic, biotic and societal features of agro-ecosystems, at a broad scale. We developed an extension to the framework that permitted some of these pathways to be explored in greater detail; Figures 2.4-2.6 display the more detailed relationships between increasing temperature, our three focal organism groups (pollinating insects, pest regulating animals, and AMF), and the ecosystem services they provide. Viewing these detailed sequences of changes highlighted several important knowledge gaps within the literature; firstly, how climate change is expected to affect species interactions at the level of the community, and how this in turn may affect delivery of ecosystem services; secondly, how reductions in the biodiversity of all three focal organism groups will affect non-crop plants; thirdly, how climate change will affect AMF diversity and abundance; and finally, how biodiversity loss will affect cultural ecosystem service delivery. We developed a second extension to the DPSIR that provided an overview of the specific changes that can be expected for each of the abiotic, biotic and societal features within the framework, based upon current literature; Figure 2.7 displays the directions of change, with levels of confidence, that the present research indicates. There is strong evidence suggesting climate change will have negative impacts on many aspects of agro-ecosystems; physical features of the environment relating to soil will deteriorate, causing increased soil erosion and carbon emissions; biodiversity will decrease in terms of distribution, abundance, and species richness, causing reductions in regulating services such as pollination; crop yields will decline, causing reduced food security; and biodiversity and habitats will be lost, causing reductions in cultural ecosystem services such as the health and well-being benefits of interacting with nature. The novel three-step methodology implemented here successfully provided additional details and assessments that extend the scope and utility of the standard DPSIR framework approach; this method would be particularly relevant for investigating other large and complex systems that are responding to environmental change.

2.4.1 The DPSIR framework

The DPSIR framework proved to be a useful tool to collate and organise information relevant to the system in question from a diverse range of sources and disciplines. However, while the framework was demonstrated to be suitable for modelling this system and topic, the creation process was quite challenging due to a number of reasons relating to variation and incongruities in the literature. Construction of the framework in this study was hindered, at least initially, by inconsistencies of approach with respect to how the DPSIR is applied to global problems and ecosystem services. Deciding on how to define climate change and where to structure it within the DPSIR presented the first challenge, as there are relevant examples in the literature of at least three different methods: define it as a Driver (Bär et al., 2015; Holman et al., 2008; Kelble et al., 2013; Roura-Pascual et al., 2009), consider it a Pressure (Omann et al., 2009; Rounsevell et al., 2010), or describe it as an 'exogenic' unmanaged Pressure (Atkins et al., 2011a; Elliott et al., 2017). Given that agriculture is a significant source of anthropogenic greenhouse gas emissions (IPCC, 2014b), and that the UK has climate change policies in place that relate to agriculture (The Committee on Climate Change, 2013) and vice versa (DEFRA, 2013), it would be illogical to consider climate change to be external to UK agro-ecosystems. The end decision to place climate change as a Driver rather than Pressure was based upon two factors: firstly, a desire to reflect the terminology used by the MEA (2005), UK NEA (2011c), UK Department for Environment Food and Rural Affairs (Brown et al., 2012; Knox et al., 2012) and the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES, 2017); and secondly, this allows the specific changes in temperature, CO_2 and precipitation to be explored as separate Pressures, which more accurately reflects the hypotheses and methods of the relevant scientific research examining climate change impacts, where many studies only investigate one of these Pressures (e.g. Liu et al., 2016; Memmott et al., 2007).

The placement of the different elements of agro-ecosystems within the DPSIR framework was also hindered by the plurality of definitions and classification systems for ecosystem processes, services, and benefits that can be found in the wider literature (La Notte et al., 2017). The interpretations of what the biological, physical and socio-economic features of systems are, can be very different between publications that are bio-centred (IPBES, 2017; MEA, 2005; UK NEA, 2011c) and those that are human-centred (Spangenberg et al., 2014; TEEB, 2010). This difference presented two problems with respect to the current

research: firstly, the human-centred viewpoint often downplays supporting ecosystem services, such as soil formation and nutrient cycling, either by shifting their focus and reclassifying them as regulating services, or by reducing them to a collection of vague functions labelled 'ecosystem processes' (or something similar) (Spangenberg et al., 2014; TEEB, 2010), both of which made it difficult to appropriately place and classify such supporting elements and their references (Boerema et al., 2017); and secondly, the two viewpoints contain blurred and/or overlapping understandings of provisioning services, final services, and goods/benefits (Boerema et al., 2017; Fisher et al., 2009; La Notte et al., 2017), which could lead to double-counting within the DPSIR framework. The first problem was relatively easy to address by choosing to align to the holistic and widely accepted MEA and UK NEA definitions of supporting services (MEA, 2005; UK NEA, 2011b). To avoid double-counting required clear and distinctive definitions of not only the relevant provisioning/final services and goods/benefits, but also the State changes and Impacts categories within which they are to be placed; this was harder to achieve due to the diverse range of approaches that researchers have employed in defining these features within DPSIR frameworks (Atkins et al., 2011a; Gregory et al., 2013; Kelble et al., 2013; Pinto et al., 2013; Rounsevell et al., 2010). Our solution was to employ a hybrid classification system for ecosystem services, incorporating all the services listed in the MEA and classifying each of them using both the holistic MEA system and a more reductionist services/goods/benefits system (see Figure 2.2), which can make clear distinctions between State changes and Impacts: the former are services that have the potential to benefit people, the latter are those benefits realised. Addressing both problems also required careful consideration for exactly what the evidence did and did not show to ensure accuracy with respect to the nature and positioning of the different elements and references within the DPSIR. These difficulties, stemming from the multiple interpretations of ecosystem services, processes and benefits employed by researchers and policy makers, highlights the wider need for greater consistency between disciplines and viewpoints with regards to the terminology, definitions and classification systems that they use (Boerema et al., 2017; La Notte et al., 2017).

2.4.2 Knowledge gaps

Drawing on evidence from the literature to create the DPSIR framework provided insight into the knowledge gaps that exist within that literature. Most of the knowledge gaps

highlighted by this study relate to how climate change is expected to affect species interactions at the level of the community, and how this in turn may affect the delivery of ecosystem services. Studying community-wide species-interactions can be very challenging due to the time and resource intensive methods required, particularly if research is undertaken in-situ and especially for organisms such as parasitoids and soil fungi that are difficult to detect and identify. Combining DNA metabarcoding approaches with network analysis represents a promising method of investigating these interactions and their impacts upon ecosystem functioning and services (Evans et al., 2016), so it is likely that these and other new techniques will offer opportunities to improve our understanding of community interactions. However, even with these new methods, it may prove difficult to find definitive causal links between climate change and changes in species interactions due to the complicated nature of community ecology, which involves studying many interacting environmental variables and species. In these situations it can be challenging to disentangle the many causes and their effects and often the results of studies investigating the same topic using different methodologies do not align, which makes it difficult to obtain clear evidence (Hegland et al., 2009; Tylianakis et al., 2008). There are also difficulties associated with measuring ecosystem service provision: for example, it cannot be assumed that every insect that visits a flower is a potential pollinator. New methods and experimental designs are being developed that should provide more accurate assessment of service delivery, such as 'single visit deposition', which should help to differentiate between pollination and visitation (Ballantyne et al., 2015; King et al., 2013). Another key knowledge gap highlighted in the DPSIR framework is a lack of research investigating how changes in the three climatic variables associated with climate change will affect biodiversity, agriculture and ecosystem services, when they are considered in concert. This is most likely due to the practicalities of investigating them; field experiments simulating either increases in temperature or CO_2 can be extremely difficult both logistically and financially at large scales, so to combine both and include changes in precipitation is probably prohibitively expensive for most ecological researchers.

Another area identified as lacking evidence is that of how changes in the abundance and diversity of specific organism groups will affect the delivery of cultural goods and services. At present, there is evidence demonstrating positive relationships between general biodiversity and the diversity of some specific organism groups, such as higher plants, to the

delivery of these services and goods in UK (see Figures 2.4, 2.5 and 2.6), but there is little or no scientific evidence linking the diversity and abundance of other organism groups, such as pollinating insects and insectivorous birds, to cultural services and goods, despite the seemingly obvious relationships. Indeed, in several of the papers that examine service delivery by birds, the authors acknowledge that birds contribute to cultural services, but they do not consider them in their research (e.g. Wenny et al., 2011; Whelan et al., 2008). This apparent lack of attention could be due to the multidisciplinary nature of the topic, given that it requires social, economic and natural science perspectives. Interest in cultural service research is increasing, so it may be that evidence linking the abundance and diversity of other organisms to cultural goods and services is on the horizon. Another key knowledge gap uncovered during this study relates to the nature of the cultural service evidence; all of the relevant literature included in our analysis investigates the presence and strength of positive relationships between biodiversity and cultural services, rather than investigating how a loss in biodiversity may negatively impact these services. It is likely that this can also be attributed to the difficulties inherent to conducting research in this field, which means that researchers are still focusing on exploration and description of the relationships. It is probable that the focus will broaden in the near future to include experimental manipulations and hypothesis testing relating to environmental change.

As well as identifying knowledge gaps in the literature, this study has also highlighted areas where there the evidence base is strong. Pollinators are a very well-studied group of organisms, there is good evidence for range, abundance and diversity declines and the different factors that influence these declines including climate change. There is a lot of evidence documenting that biodiversity is affected by climate change, particularly in terms of species range shifts and changing phenology (Parmesan, 2006). The subject of how crop yields are likely to be impacted by climate change is an area where research historically failed to produce a consensus despite the popularity of the topic, but recent approaches are producing more consistent findings that demonstrate an overall negative impact (Asseng et al., 2015; Cai et al., 2015; Liu et al., 2016).

2.4.3 Directions of change

The directions of change shown in Figure 2.7 provide a striking representation of how current projections of future climate change will impact the environment, biodiversity and

ecosystem services of the UK and other temperate developed countries, given the knowledge gaps and uncertainty. It is likely that many of the ecosystem services associated with agro-ecosystems will be down-regulated, and that the availability of the goods and benefits that humans receive from these environments will decline. The evidence for negative impacts upon biodiversity and habitats is particularly strong and concerning, as is the evidence for increased environmental degradation such as soil erosion. Another troubling issue is that of crop yields; there is now strong evidence indicating that yields will decrease significantly as a direct result of temperature increases, but the predicted ecological and environmental degradation and reductions in ecosystem service delivery, combined with increases in pest organisms and frequencies of extreme weather events, are extremely likely to further impact agricultural production and food security. Yet these predictions are not certainties; there is still time to put into practice measures that could ameliorate some of these negative effects and increase the resilience of agro-ecosystems to climate change.

The UK National Adaptation Programme is a key policy document contained in the Response category of the DPSIR framework (Figure 2.3); it details the specific measures that government plan to put in place to increase the resilience of both the UK's natural and agricultural environments to climate change (DEFRA, 2018a). This plan is designed to address the risks highlighted by the Climate Change Risk Assessment Evidence Report (Brown et al., 2016), which was written by a committee of expert academics at the request of the government. However, there is one key area that the scientists highlighted as at risk that the government politicians disagreed with: food security (UK Government, 2017). As a result of this disagreement, there are several risks to UK food security and prices identified by the scientists as high priorities, which the Adaptation Programme completely ignores; these risks relate to uncertainties regarding global food production, trade and supply chains. The UK government has chosen not to take proactive measures and, perhaps over-optimistically, believes that international food production and supply chains are resilient enough to cope with future climate change impacts. While these contentious risks are beyond the boundary of our DPSIR framework, they are still relevant here given the possibility that reductions in domestic production may put greater pressure on global supply chains. Regardless of the views on international food production, there are several direct measures planned that will attempt to safeguard domestic food production. The UK government is focussing on

improving development and implementation of novel agricultural technologies by entrenching climate change adaptation within agriculture research programmes, stimulating collaboration between industry and academia, and offering farmers grants to purchase new technology and equipment (DEFRA, 2018a).

The UK government is currently in the process of developing a new Environmental Land Management System that includes aims relevant to the findings of our research: increase biodiversity, improve soil quality and increase climate change adaptation and mitigation (DEFRA, 2018a; UK Government, 2018). It is not yet clear exactly how this system will achieve these aims, but the National Adaptation Programme includes several specific measures that will be part of it (DEFRA, 2018a). Biodiversity will be increased via a targeted approach to agri-environment schemes that aims to improve the extent and connectivity of habitats in farmland. Indeed, the government has pledged to restore and create 500,000 ha of wildlife-rich habitat outside of protected areas. In addition, the government plans to provide increased protection for species and habitats that are particularly vulnerable to climate change, and to work with major landowners to ensure their management and conservation activities address climate change. Soil quality will be improved by two measures working in tandem: guidance on management practices such as tillage and cropping will be updated and improved, and soil quality monitoring will be made easier and more accessible to land managers via a new soil health index, which will allow the effectiveness of the management practices to be assessed. It is also likely that a targeted approach to soil quality improvement that involves novel agri-environment schemes will be developed, as there are several statements in the National Adaptation programme that mention incentivising farming methods that improve soil quality and stability. The previous National Adaptation Programme suggested that a 'payment for ecosystem services' approach could be a viable way to safeguard the natural environment in the face of climate change (DEFRA, 2013) and it is possible that the new Environmental Land Management System currently in development will employ such tactics, given that it will be underpinned by natural capital principles (UK Government, 2018).

Aside from opportunities for adaptation and mitigation, there are also opportunities for climate change prevention. We know that our climate is committed to a certain level of warming due to the CO_2 that has already been emitted, and that which will be emitted in the near future (IPCC, 2013), but what is less certain is how our climate will change further into

the future; if we can make sufficient changes now to reduce greenhouse gas emissions then further climatic changes could be prevented. The National Adaptation Programme and the Environmental Land Management System will address carbon storage via the previously described activities that will improve soil quality and restore habitats (DEFRA, 2018a; UK Government, 2018), but there also needs to be a greater focus on renewable energy and increased investment in related research and technology. There are also many aspects of modern society where changes could be made that would provide multiple benefits to both humans and our environment, such as: reducing food waste, reducing obesity, eating less meat, and using more environmentally-friendly transport. These suggestions all require top-down policy support and cooperation between politicians, industries and researchers, and to be truly effective they must be implemented at the global scale. The United Nations Paris Agreement (UN, 2016) appears to be a good start, with 195 signatories agreeing to three main actions: "(a) holding the increase in the global average temperature to well below 2 °C above pre-industrial levels and to pursue efforts to limit the temperature increase to 1.5 °C above pre-industrial levels…; (b) increasing the ability to adapt to the adverse impacts of climate change and foster climate resilience and low greenhouse gas emissions development, in a manner that does not threaten food production; (c) making finance flows consistent with a pathway towards low greenhouse gas emissions and climate-resilient development." These aims would certainly safeguard natural environments and agro-ecosystems if they were achieved and some countries are implementing the Agreement with new policies, such as recent announcements by the governments of several European countries to ban all petrol and diesel vehicles in the near future. Unfortunately, there remain many uncertainties due to the shifting global political climate, which is highlighted by the recent withdrawal of the USA from the Paris Agreement by President Trump, and the impending withdrawal of the UK from the European Union.

2.4.4 Limitations

The DPSIR framework was constructed using a literature review approach that drew on evidence from the agricultural, social, economic, and natural science literature, and from various policy documents. While this method creates a reliable and evidence-based DPSIR, it is possible that it may not be completely comprehensive as there could be relevant features and relationships that have not yet been described or suggested within the wider published

literature. Additionally, while the use of a multidisciplinary research team (comprising two terrestrial ecologists and one environmental economist) provided an effective check for the relevance of the evidence before its inclusion, it is possible that our combined expertise were not broad enough to identify all the relevant evidence or relationships from beyond the literature of our fields of study. However, it is unlikely that any features or relationships relevant to climate change and agro-ecosystems were omitted from the DPSIR, due to the extremely thorough background reading undertaken by the lead researcher, and the use of the MEA, UK NEA and UK Government climate change risk assessment reports (Brown et al., 2016, 2012; Knox et al., 2012; MEA, 2005; UK NEA, 2011c), all of which have very broad scopes, as a starting point for the literature review. Nevertheless, it could be argued that involving other members of the stakeholder community associated with UK agro-ecosystems, ecosystem services, or climate change could have offered the potential for a stronger check on both the coverage of the DPSIR framework and the evidence it relied upon. While stakeholder participation was not deemed to be necessary or cost-effective in the present context, further work building on this research could involve stakeholder consultation, if only to validate/correct the results of the present study.

The aim of the second step of the analysis was to show some of the cause and effect relationships in more detail, providing a clear sequence of consequences stemming from climate change. However, while Figures 2.4-2.6 do display this greater definition, it is at the cost of comprehensiveness due to the focus on only one organism group at a time, and only one Pressure. The reality of the system is far more complicated with multiple linkages between the Pressures, different abiotic and biotic features of the environment, and the different ecosystem services, but attempting to show all this information accurately would be extremely difficult to achieve whilst still retaining intelligibility (for example, see Figure 2.S1 in appendix 2.6 for a combined version of Figures 2.4-2.6). Regardless of the compromise we made in terms of how we carried it out, this second step of the analysis represents an added layer of detail to the standard DPSIR method and proved suitable for the present study's aims.

2.4.5 Conclusions

Food security and biodiversity loss are serious and potentially conflicting global problems that cannot easily be resolved, particularly with the threat of climate change

becoming increasingly more urgent. The DPSIR framework proved suitable for modelling UK agro-ecosystems and climate change, but difficulties with structuring the framework highlight the need for greater consistency between disciplines and viewpoints with regards to the terminology, definitions and classification systems that are employed with respect to ecosystem services. We developed a novel and iterative three-step approach that allowed exploration of the climate change impacts at both broad and narrow scales. The DPSIR constructed in this study has identified several topics that require further investigation, including the impacts that climate change will have on community interactions across trophic levels and the resulting changes to ecosystem service delivery. The directions of change in Figure 2.7 provides a stark overview of how negatively climate change will impact our environment, biodiversity and ecosystem services, even with the knowledge gaps and uncertainties identified in this paper. These knowledge gaps represent opportunities that researchers and funding organisations need to capitalise on – addressing these issues would provide an even stronger case for biodiversity conservation and protection of our natural environments.

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2.6 Appendix

Table 2.S1 References used to create the DPSIR framework and the corresponding numbers used to denote them in Figures 2.3, 2.4, 2.5 and 2.6 (displayed over 4 pages)

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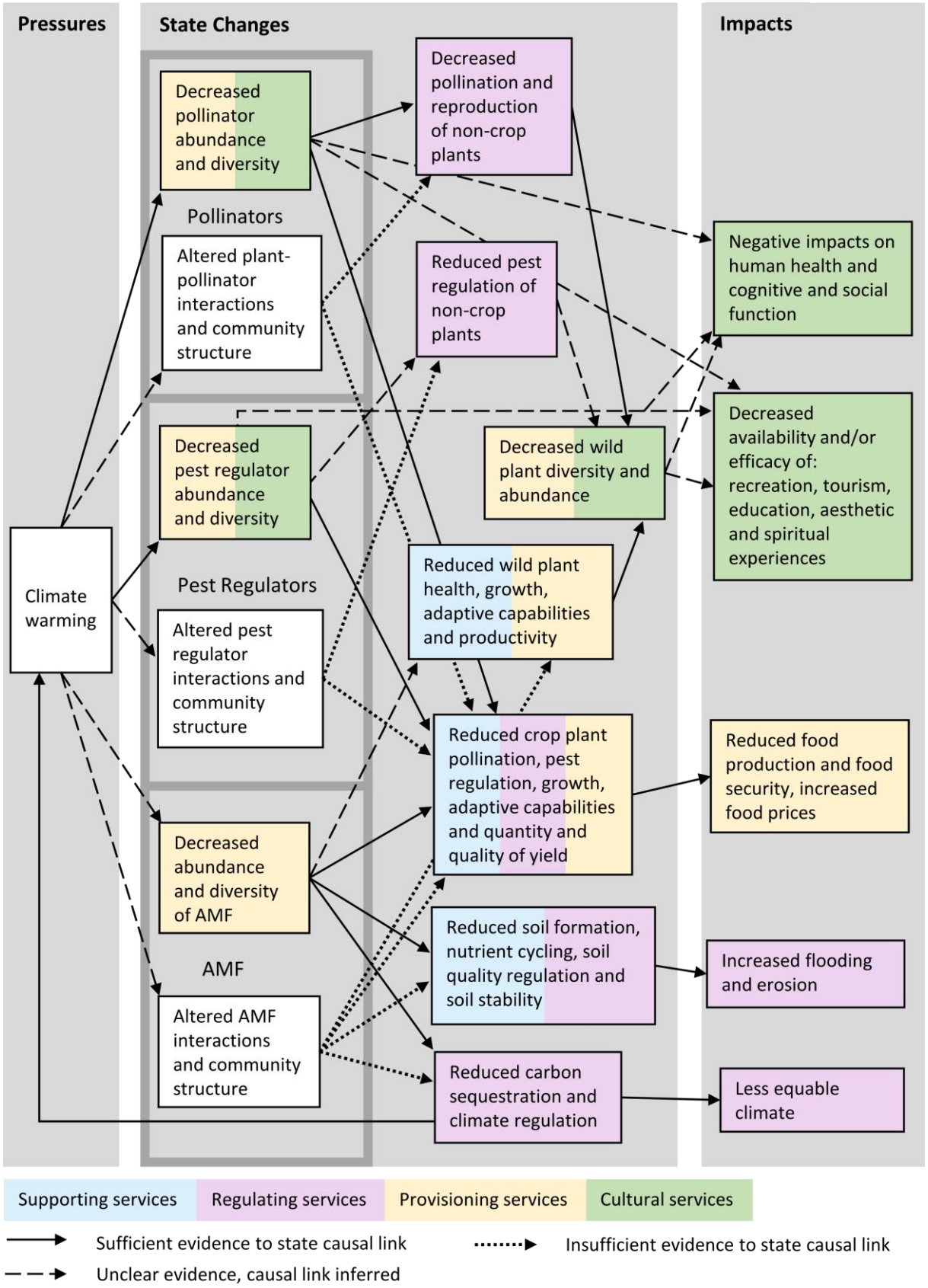
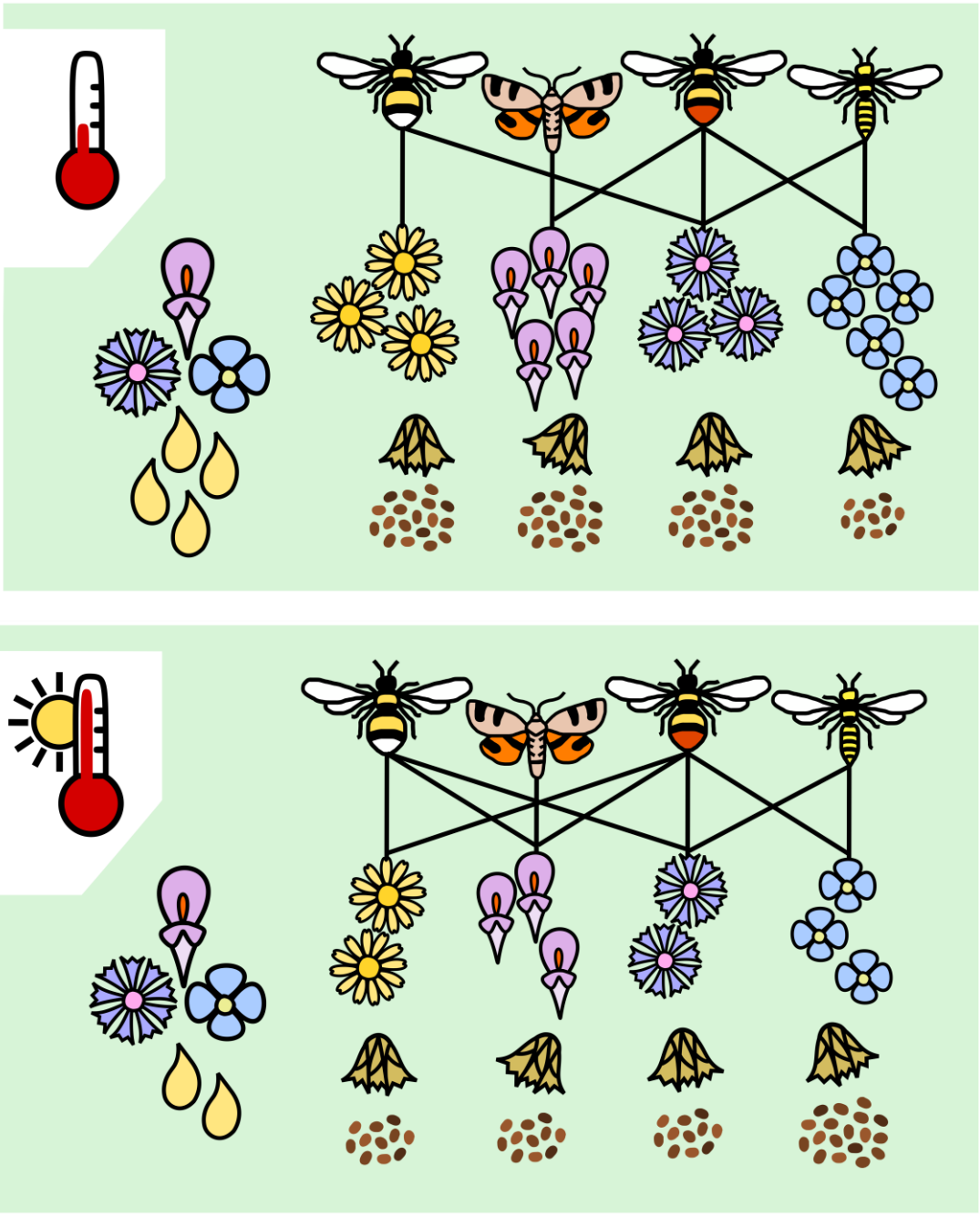


Figure 2.S1 A more detailed examination of how climate warming impacts the ecosystem services provided by pollinating insects, pest regulating animals, and AMF. Created by combining Figures 2.4, 2.5 and 2.6.

Chapter 3. Investigating the effects of simulated climate-warming on floral resources, insect visitation and wildflower seed set in a cereal agro-ecosystem



Abstract

Declines in pollinating insects and wildflowers have been well documented in recent years, caused by multiple factors such as agricultural intensification and land use change. Climate change is expected to exacerbate these declines, but little is known about how whole communities will be affected and what impacts there may be on the provision of ecosystem services such as pollination. Ecological networks characterise the relationships between interacting species and describe community structure, stability and ecosystem function. Using a fully replicated open-air field experiment we simulated an increase in temperature of 1.5 °C and rainwater of 40% for two growing seasons to investigate how climate change may impact several within-field features of temperate arable agro-ecosystems: (1) floral resources of arable wildflowers for insects; (2) insect visitation; (3) flower-visitor network structure; and (4) wildflower seed set. Simulated warming reduced floral abundance by nearly 40%, and nectar volumes were reduced by over 60% for two species. Species richness of plants and insects were unaffected by warming, while visitor abundance and community composition were both affected in the first growing season, but not in the second. Simulated warming significantly increased the frequency of visits to flowers. The complexity of the flower-visitor networks was significantly increased under warming, but the consumer-resource asymmetries and structural evenness were unaffected. Wildflower seed set was significantly affected for all five species examined, with reductions in seed number and/or seed weight for four of them. These findings not only demonstrate the potentially adverse impacts that climate change might have on arable wildflowers and the pollinating insects that feed on them, but also how the cumulative effects of subtle changes can affect community interactions and ecosystem functioning.

3.1 Introduction

Wild insect pollinators are important to human nutrition, economics, ecosystems and agriculture (Eilers et al., 2011; Gallai et al., 2009; Garibaldi et al., 2013; Klein et al., 2007; Ollerton et al., 2011), so there have been concerns over recent declines in pollinator species diversity and abundance (Biesmeijer et al., 2006; Cameron et al., 2011; Fox, 2013; Potts et al., 2010a, 2010b). These declines have been attributed to a number of factors such as agricultural intensification, land use change, and disease (Cameron et al., 2011; Kennedy et al., 2013; Senapathi et al., 2015; Tscharntke et al., 2005). With global temperatures expected to rise by at least 2 ^{o}C by the end of the 21st century (relative to 1850-1900) (IPCC, 2013), climate-warming is expected to compound these pollinator declines by causing range shifts and phenological changes, with some recent evidence for bumblebee convergence across continents (Kerr et al., 2015). In particular, there is concern regarding how changing phenologies and distributions of plants and their pollinators may lead to temporal and spatial mismatches between them (Hegland et al., 2009). While there are few empirical studies that have examined this topic, most of the current evidence suggests where such mismatches do occur they may be less detrimental to community structure and ecosystem functioning than initially feared (Rafferty and Ives, 2011; Willmer, 2012). However, it is as yet unclear how climate change will impact whole pollinator communities and their interactions with flowering plants due to a lack of experimental evidence (Hegland et al., 2009; Scaven and Rafferty, 2013), or what the consequences are for ecosystem services and functioning.

To date, most studies have looked at how climate change affects individual species or a subset of wild pollinators (Parmesan, 2006); these approaches have yielded valuable insights into how groups such as butterflies (Parmesan et al., 1999) and bumblebees (Kerr et al., 2015) are responding to climatic changes by shifting range to track optimal conditions, and how some pollinators are advancing phenologically (Bartomeus et al., 2011; Hassall et al., 2017). However, these insects do not exist in isolation, therefore it is crucial to examine how climate change will affect entire communities of interacting plants and animals to gain a better understanding not only of biodiversity responses, but also the impacts on important ecological processes, such as pollination. Species-interaction networks are well suited to investigating such questions as they characterise community structure and the underlying ecosystem stability and functioning (Montoya et al., 2006), allowing the assessment of how many small changes at the species level can add up to significant community scale impacts

(Scaven and Rafferty, 2013). However, few studies have examined the response of ecological networks to climate-warming. Memmot et al. (2007) looked at how phenologies could become mismatched under increased atmospheric CO_2 concentrations using a modelling approach and found that a reduction in food for pollinators during crucial periods will lead to extinctions of both plants and pollinators, though a more recent interaction study found no experimental evidence of temporal mismatches (Rafferty and Ives, 2011). Burkle et al. (2013) examined long-term observational datasets of plant-pollinator interactions and found evidence of temporal and spatial mismatches and changes in network structure, though it is not clear how much this can be attributed to climate change as the study site also experienced land use change. More recently Hoiss et al. (2015) used an experimental approach employing an altitudinal gradient as a climate warming proxy in combination with simulated drought and early snow melt treatments to investigate how plant-pollinator network structure could be affected by climate change; they found the degree of network specialisation decreased with increasing elevation, but was only affected by extreme climatic events for generalised networks, which suggests that high generalisation within a network does not guarantee stability. The approaches used in these studies have yielded valuable insights into how climatic changes may affect plant-pollinator networks, but they lack temporal and spatial replication and so far, there have been no experiments, to our knowledge, simulating climate-warming in natural field conditions.

An increasing body of research has looked at how pollinator loss affects pollination and ecosystem functioning, with studies finding links between pollinator visitation and wildflower seed set (Franzén and Larsson, 2009; Lundgren et al., 2013), crop yield (Garibaldi et al., 2013; Garratt et al., 2014b), seedling recruitment (Lundgren et al., 2015), and seedling diversity (Lundgren et al., 2016). However, very few studies have investigated this in the context of climate change. Kudo & Ida (2013) examined how phenological mismatches between an early spring wildflower and its bumblebee pollinators affected seed set; they found the plant and pollinators displayed differing sensitivity to early onset of spring, which caused phenological mismatches, and this in turn led to reduced seed set. Thomson (2010) found evidence of increasing asynchrony and pollination limitation between an early sub-alpine plant and its bumblebee pollinator. As well as looking at plant-pollinator networks in their long-term observational study, Burkle et al. (2013) also quantified how the number of pollen grains carried by bees caught at their site was affected over time; their results

showed a decline in pollination service but it is unclear how much of this effect can be attributed to climate change rather than land use change. Bishop et al. (2016) examined heat stress events and found that insect pollinators were able to recover yield losses in faba bean (*Vicia faba*) crops after moderate heat stress. It is therefore possible that increased pollinator visitation could offset the negative effects of climate warming on plant reproduction, at least for some species.

We established a fully-replicated, simulated climate-warming experiment on a UK arable farm to examine the impacts of elevated temperature and increased rainwater on agricultural plants and flower-visiting insects, over two spring/summer growing seasons. Temperature was increased by 1.5 °C, which aligns with current climate projections for Northern Europe and weather models for the UK (IPCC, 2013; Kendon et al., 2014). Precipitation was increased by 40% and this can either be interpreted as representing weather conditions in a warm and wet summer, or a farmer increasing irrigation to mitigate the effects of a warmer and drier summer. The experimental method employed uses a bottom-up approach, whereby only the lowest trophic level (plant life) is manipulated directly, but resultant changes in flower-visiting insects and species interactions can be observed in addition to the responses of the plants (Scherber et al., 2010). Our experiment had four main objectives: (1) To investigate how simulated climate-warming affects arable wildflower floral resources. We predicted that warming would negatively affect the floral resources of the wildflower species; there is limited evidence indicating that increases in temperature can lead to reductions in both the number of individual plants and flowers per plant (Liu et al., 2012; Saavedra et al., 2003), as well as altering floral nectar volumes, concentrations and sugar ratios (Hoover et al., 2012; Pacini et al., 2003; Walker et al., 1974); (2) To observe any changes in insect visitation. Given the bottom-up approach and open-air nature of the experiment we expected that there would be no changes in the flower-visitor community *per se* but that other factors, such as foraging behaviour, could be affected by a reduction in floral resources (Fowler et al., 2016); (3) To examine the impacts of climate warming on plant-insect network structure. We predicted that any changes in floral resources would have knock-on effects on the structure and/or complexity of plant-flower visitor networks; changes in floral abundance and quality combined with changes in pollinator behaviour would affect interaction strength and alter network structure and dynamics (Scaven and Rafferty, 2013), and changes in phenology have been shown to affect

network structure (Burkle et al., 2013; Memmott et al., 2007) ; (4) To investigate how experimental warming affects wildflower seed set. We predicted that simulated warming would negatively impact the seed production of the wildflower species; there is considerable evidence indicating that crop yields will decrease as a result of increasing global temperature (Liu et al., 2016) and there is some evidence for non-crop plants (Jin et al., 2011), although it is possible that this could be offset by increased insect visitation.

3.2 Methods

3.2.1 Experimental approach

The experiment was conducted at Stockbridge Technology Centre (STC) in North Yorkshire (53°49'N–1°9'W). It is a conventional farm consisting of fallow and crops grown both commercially and for agricultural research. The surrounding landscape is typical of this area of Yorkshire: very little altitudinal variation, frequent agricultural drainage channels, predominantly rural character, and dominated by arable farming with little by way of semi-natural habitat. While STC grows a relatively high variety of both cereal and horticultural crops in relatively small field sizes, the surrounding farms are more conventional, with larger fields and a lower crop diversity (mainly cereals and oilseed rape). STC also has a higher proportion of semi-natural habitat than the surrounding farms.

Our experimental setup and manipulations replicated those of Rollinson and Kaye (2012); full details of the simulated climate-warming experiment can be found in Berthe et al. (2015). Briefly, the experiment consisted of 24 outdoor 2 x 2 m plots in an agricultural field, separated by 2m buffers, in a randomised block design with 6 replicates of four treatments: 2 °C increase in temperature above ambient ('HEAT'); 40% increase in precipitation ('WATER'); warming and precipitation treatments combined ('HEAT+WATER'); and ambient conditions ('CONTROL') (See Figure 3.S1 in appendix 3.6.1 for experimental layout). The temperature increase was targeted at 2 °C, but a mean increase of 1.5 °C was actually achieved during the experiment. The heated plots were warmed with 165 x 15 cm infra-red heaters suspended 1.5 m above them operating continuously from the date of assembly in spring, until the end of sampling at the end of summer (16/04/14 - 19/08/14 and 15/04/15 - 18/08/2015). The unheated plots had 'dummy' heaters suspended above them that were matched for shape and size to the real heaters to mimic any potential shading effect.

Infrared temperature sensors monitored the soil surface temperatures in the heated and unheated plots, these were connected to a real-time proportional-integrative-derivative (PID) feedback system (a computer housed in a wooden shelter adjacent to the plots), which was also connected to, and could control, each of the heaters. This setup allowed the PID computer to automatically maintain a constant temperature difference between the heated plots and the ambient air temperature, 24 hours per day, simply by switching the heaters on/off as necessary, according to the readings from the temperature sensors. These are non-convective heaters that directly heat soil and vegetation rather than increasing air temperature and similar radiant heaters have been shown to increase soil temperatures and advance plant phenology (Dunne et al., 2003). This bottom-up approach, of open-air heating of soil and vegetation, necessitated examination of how the insects responded to changes in the plants, rather than how the treatments impacted the insects directly. The 40% increase in precipitation was simulated by distributing collected rainwater using a watering can; volumes were based on mean monthly rainfall data collected between 2002 and 2012 at the farm's weather station. Each week the following quantities of rainwater were applied to the plots belonging to the precipitation treatments: 13L in April, 19L in May, 24L in June, 26L in July, and 30L in August.

Each year, just prior to equipment assembly, the plots and buffers were sown with spring wheat (*Triticum aestivum* cultivar Tybalt) and the plots were additionally sown with an arable wildflower seed mixture using quantities that are appropriate for establishing a grass/wildflower meadow in $4m^2$ (see Table 3.S1 in appendix 3.6.1 for species list, sowing dates and sowing weights). Eight wildflower species were selected based on several criteria: insect pollinated, native to the UK (or naturalised historic introductions from continental Europe), annual, found in arable fields, and able to grow in a within-crop habitat (Fitter and Peat, 1994; Rose and O'Reilly, 2006). We were additionally restricted to species that were commercially available as seeds from UK stock. No pesticides were applied to the plots after sowing; while this is not representative of conventional farming practices, our intention was to examine the full range of potential crop and non-crop plant-insect interactions. Invasive non-crop plants were controlled by hand weeding each plot for 10 minutes each week until the wheat and wildflowers had established, but non-sown flowering species were allowed to grow and flower.

3.2.2 Data collection and Statistical Analysis

All plant and insect samples were collected during spring and summer of 2014 and 2015. We describe specific sampling methods under each objective below. Sampling took place between the start of flowering in early June and the end of August (i.e. harvest) when the equipment was switched off. Systematic plot sampling was carried out in seven sampling rounds in both years and these dates were matched as closely as possible to ensure even sampling between years.

All of the flower visitor data, interaction network data, and several of the plant datasets (floral abundance and richness) were collected at the plot level. In order to boost the subsequent small sample sizes both years of data were combined, and these datasets were then analysed with generalised linear models (GLMs), which included a 'treatment:year' interaction term. Significant effects of treatment and year were determined via ANOVA run on these GLMs, all using R version 3.2.3 (R Core Team, 2015). Where the interaction term was non-significant the models were re-run without it. The degrees of freedom for all the significance tests were the same for each element: treatment = 3, year = 1, treatment:year interaction = 3. The nectar and seed datasets were collected in a way that produced multiple values per plot. As a result, these datasets were analysed using mixed effects models via the 'lme4' package (Bates et al., 2015), where treatment was a fixed effect and plot a random effect. Significant effects of treatment were determined via likelihood ratio tests, where the degrees of freedom were always 3. For all datasets and all variables detailed hereafter, selection of error distribution families was based firstly on the type of data to be analysed (such as integer, decimal, percentage etc.), and secondly on the distribution of the data and the fit of the models they produced. Where a Poisson model was overdispersed, a quasipoisson or negative binomial error family was used instead (the latter when overdispersion was very high). Descriptions of these models including the error families are given below.

3.2.3 Objective 1: Investigating the effects of simulated warming on wildflower floral resources

All flowering plant species (including non-sown species) were identified and floral units were counted (Forup et al., 2008) in each plot during each sampling round. Abundance of individuals of each plant species was not recorded as it was too difficult to determine without causing extreme disturbance and damage within the plots, due to the intertwined

and tangled way that the plants grew. There were two additional floral sampling events for nectar collection in 2015. In mid-June, during flowering of the early species (*Lamium purpureum, Stellaria media and Veronica persica*), 5 flower buds from these three species in each plot were bagged with small fine mesh drawstring bags and nectar volume was sampled using 0.5 microL microcapillary tubes once the flowers had opened (Kearns and Inouye, 1993). This process was repeated in late July for the later-flowering species (*Centaurea cyanus* and *Glebionis segetum*). Nectar was unobtainable from *S. media* and *G. segetum* due to the nectaries being too small for the microcapillary tubes available.

To examine plant diversity, raw species richness values were used as the plots were searched exhaustively for plant species every fortnight. Only flowering plant species were considered for analysis. Floral abundance for each plot was summed across sampling rounds to give a total for the whole season (it is possible that some flowers may have been counted twice, but very unlikely because repeat surveys of plots were at least a week apart). Species richness and floral abundance were analysed using GLMs with Poisson and Gaussian error respectively. Nectar volumes were analysed using mixed effects models with Gaussian error for *V. persica,* Gamma error for *L. purpureum*, and inverse Gaussian error for *C. cyanus.* Community dissimilarities for flowering plants across the treatments were assessed via the Bray-Curtis method using the adonis function of the 'vegan' package (Oksanen et al., 2016) for R.

3.2.4 Objective 2: Assessing the effects of simulated warming on flower visitation

Plot observations were carried out to sample flower-visiting insects; each of the experimental plots was observed for a total of 20 minutes per sampling round, during which, insect specimens were caught using a hand-net and euthanised with ethyl acetate in individual tubes. All insect samples were later identified in a laboratory to species level, or as close to as possible, by taxonomists using morphological keys (Ball, 2008; Chinery, 2012; Collin, 1961; d'Assis Fonseca, 1968; Else and Edwards, 2018; Prys-Jones and Corbet, 2011; Stubbs and Falk, 2002; Yeo and Corbet, 1995). Sampling occurred on any and all wildflowers present in each plot, which included non-sown species. Sampling took place between 9:00-17:00 (Rasmussen et al., 2013) and during appropriate weather: temperatures of at least 15 ^{o}C, no more than a slight wind, and no precipitation (Forup et al., 2008; Garratt et al., 2014a).

Species accumulation curves were created for each plot to examine sampling completeness of insect visitors. Asymptotes were not reached so species richness was extrapolated and Chao estimates (Chao, 1987) of richness calculated using package vegan in R. Diet breadth was calculated across all visitor species visiting each plot, as the mean number of plant species each pollinator species visits, generating one mean diet breadth value per plot. Frequency of visits to flowers was also calculated for each plot (visits/flowers), it was also calculated for two of the sown species that had sufficient visitation data: *G. segetum* and *C. cyanus*. Extrapolated species richness, diet breadth and visits per *G. segetum* flower were analysed using GLMs with inverse Gaussian error; visitor abundance with a quasipoisson error; visits per *C. cyanus* flower with Gaussian error, and visits per flower (all species combined) with Gamma error. Community dissimilarities for insects across the treatments were also assessed via the Bray-Curtis method using the adonis function of the 'vegan' package.

3.2.5 Objective 3: Investigating the impact of simulated warming on networks

During plot observations, only specimens that were seen interacting with the reproductive parts of the flowers while feeding were caught (Alarcón et al., 2008); this ensured that the data would be suitable for constructing flower-visitor species interaction networks.

A species interaction network was constructed for each plot and network descriptors calculated, using the 'bipartite' package in R (Dormann et al., 2008). Four quantitative network metrics (Bersier et al., 2002) appropriate for mutualistic networks were chosen to examine changes in network complexity (Weighted Connectance (C_q): the number of potential interactions that are realised), consumer-resource asymmetries (Generality (G_q): the number of flower species per visitor species, Vulnerability (V_q): the number of visitor species per flower species), and evenness of structure (Interaction Evenness: how even the frequency of the different interactions is). Generality and Vulnerability were analysed using GLMs with Gaussian error. Because both Weighted Connectance and Interaction Evenness are bound by 0 and 1, they were analysed using beta regression with the 'betareg' package (Cribari-Neto and Zeileis, 2010) and likelihood ratio tests using the 'lmtest' package (Zeileis and Hothorn, 2002). A conservative Bonferroni correction was applied to all the network

descriptor results as some of these variables are intercorrelated due to some overlap in the different network properties that they are calculated from (Tylianakis et al., 2007).

3.2.6 Objective 4: Evaluating the effects of simulated warming on wildflower seed set

Seed heads of three sown wildflower species (cornflower (*C. cyanus*), corn marigold (*G. segetum*) and red dead nettle (*L. purpureum*)) and two resident species (field speedwell (*V. persica*) and common chickweed (*S. media*)) were collected for seed set and seed weight analysis. Collection for each species occurred once there were at least 10 ripe and unopened seed heads present in all the plots (unfortunately the early spring species (*L. purpureum, V. persica, S. media*) were not sampled in time in 2014 due to logistical constraints). Each collection involved randomly selecting 5 ripe seed heads from each plot; these were stored separately in envelopes before being dried out in an oven at 80^{o}C for 48 hours to control for any weight differences due to additional water content caused by the watering treatments. Seed heads were processed individually: all undeveloped seeds and non-seed structures were removed, developed seeds were counted, and then a dry weight measurement of all seeds was taken and average seed weight calculated (mg). For *G. segetum*, only 3 seed heads were processed from each plot; this subsampling was necessary as processing these seed heads was extremely time consuming. In 2015, there were not enough *C. cyanus* plants and seed heads to sample five per plot, so 3 were collected and processed instead. *L. purpureum* produces a maximum of only four seeds per seed head (Fitter and Peat, 1994) and during seed collection for this species it was determined to be too difficult to differentiate between seed heads with fewer than four seeds due to some seeds falling out and those where fewer seeds had developed; as a result seed number for this species was not analysed.

Two out of the five species of wildflower had multiple years of data available (*C. cyanus* and *G. segetum*), but these were analysed separately for each year due to uneven sample sizes and to maintain consistency in the analysis method across the dataset. All seed data were analysed using mixed effects models with Gaussian error except for: 2015 *C. cyanus* seed weight (inverse Gaussian), 2014 *G. segetum* seed weight (inverse Gaussian) and *V. persica* seed weight (Gamma).

3.3 Results

Average monthly temperatures in 2014 for June, July and August were 16.1, 18.6 and 16.1 ^{o}C respectively, while the average temperatures for the same months in 2015 were 14.6, 16.8 and 17.4 ^{o}C respectively.

3.3.1 Objective 1: Investigating the effects of simulated warming on wildflower floral resources

A total of 27,326 flowers from 25 different plant species were counted in 2014 and 37,066 flowers from 19 plant species in 2015 (see Table 3.S6 in appendix 3.6.3 for a species list). There was no significant difference in the plant community between the treatments in either year (2014: F=1.124, p=0.394, 2015: F=1.659, p=0.084). In 2014, the most abundant flowers were those of *G. segetum* (8554), followed by *C. cyanus* (4102), *V. persica* (3676), *Capsella bursa-pastoris* (1662), *S. media* (1516), and *L. purpureum* (1491). The most abundant species in 2015 were the same as for 2014, but the floral abundances for some varied considerably: *G. segetum* (19180), *L. purpureum* (5619), *V. persica* (3639), *S. media* (3271), *C. bursa-pastoris* (2015), *C. cyanus* (1080). Although flowering plant species richness was unaffected by treatment (Table 3.1), it was significantly affected by year ($\chi 2$=24.851, p<0.001), with more species recorded in 2014. There was a significant effect of treatment (F=7.035, p<0.001) and year (F=9.736, p=0.003) on total floral abundance, but the interaction was not significant (Table 3.1). Floral abundance was significantly lower in the two heated treatments compared to CONTROL; 37.5% and 35.9% lower in the HEAT and HEAT+WATER treatments respectively (Figure 3.1). Climate warming reduced the nectar volumes of *L. purpureum*, *V. persica* and *C. cyanus*; volumes were 72.5%, 64.7% and 13.8% lower in the HEAT treatment vs. CONTROL respectively (Figure 3.2). These reductions were statistically significant for *L. purpureum* and *V. persica*, though not for *C. cyanus* (test statistics are in Table 3.S5 in appendix 3.6.2).

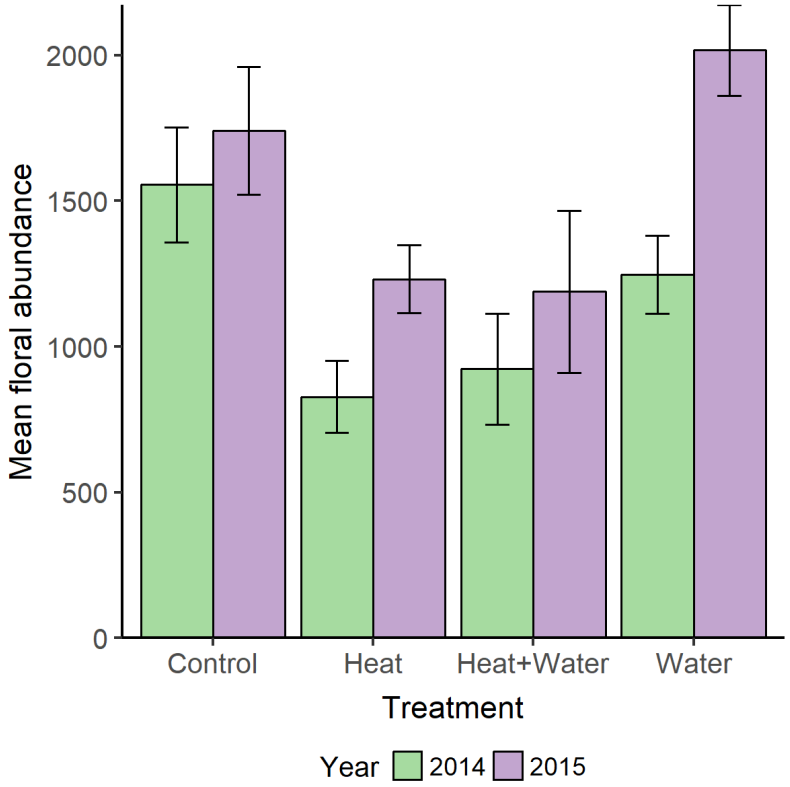


Figure 3.1 Mean floral abundance for each treatment in both sampling years, with standard error bars.

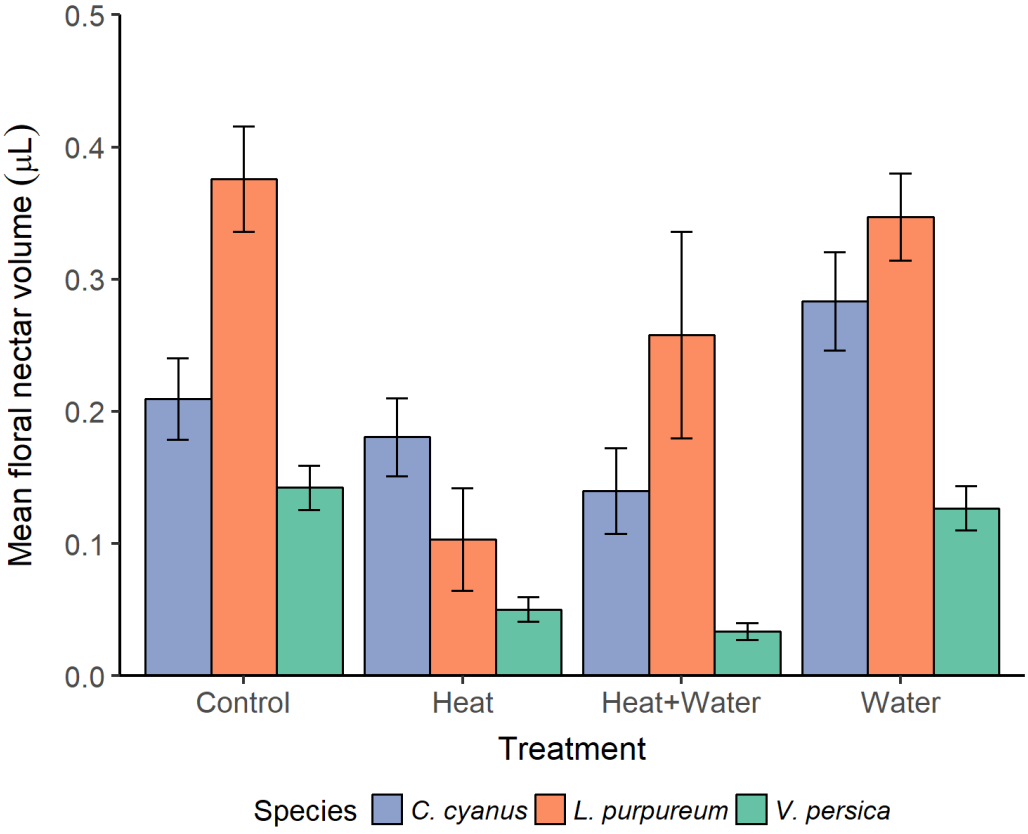


Figure 3.2 Mean nectar volumes per flower for each treatment, for three wildflower species, with standard error bars.

Variable	Treatment	Mean	Effect Size	Treatment P	Year P	Interaction P
Flower species richness	Control	12.2500 ± 0.9857	3.1249 ± 0.1465	0.510	*<0.001*	0.785
	Heat	10.3333 ± 1.0684	-0.1702 ± 0.1219			
	Heat+Water	11.6667 ± 0.7914	-0.0488 ± 0.1181			
	Water	12.0000 ± 0.6396	-0.0206 ± 0.1173			
Total floral abundance	Control	1648.3330 ± 143.2510	1039.5800 ± 234.4700	*<0.001*	*0.003*	0.408
	Heat	1029.7500 ± 101.1571	-618.5800 ± 183.9400			
	Heat+Water	1056.1670 ± 165.4637	-592.1700 ± 183.9400			
	Water	1631.7500 ± 151.5542	-16.5800 ± 183.9400			
Visitor species richness (extrapolated)	Control	36.1285 ± 4.5008	0.0008 ± 0.0004	0.812	0.898	0.485
	Heat	36.9554 ± 4.8247	0.0000 ± 0.0003			
	Heat+Water	35.7271 ± 6.1741	0.0000 ± 0.0003			
	Water	42.5849 ± 5.9898	-0.0002 ± 0.0003			
Visitor abundance	Control	85.5000 ± 4.6360	4.4490 ± 0.2009	0.660	*<0.001*	*0.042*
	Heat	78.5833 ± 8.0137	-0.8581 ± 0.3062			
	Heat+Water	76.9167 ± 7.4269	-0.7576 ± 0.3050			
	Water	82.5000 ± 4.6229	-0.3071 ± 0.2911			
Visits per flower *	Control	0.0553 ± 0.0040	17.7696 ± 2.6684	*<0.001*	0.880	0.185
	Heat	0.0794 ± 0.0077	-5.4886 ± 2.1055			
	Heat+Water	0.0863 ± 0.0102	-6.4892 ± 2.0523			
	Water	0.0540 ± 0.0046	0.4258 ± 2.4725			

* Visits per C. cyanus and G. segetum flower are in table S4.

Table 3.1 Effect of treatments on flower and insect visitor abundance and richness for both field seasons combined. Mean values are of the raw data. Effect sizes and P values of Treatment and Year are taken from models without the interaction term unless it was significant. Effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

3.3.2 Objective 2: Assessing the effects of simulated warming on visitation

A total of 1687 flower visits from 80 different insect species were recorded in 2014 and 2195 flower visits from 69 insect species in 2015 (see Table 3.S7 in appendix 3.6.3 for a species list). There was a significant difference in the insect community between the treatments in 2014 ($F=0.186$, $p=0.032$) but not in 2015 ($F=0.151$, $p=0.214$). In 2014, the most abundant insect groups were hoverflies (Syrphidae) (1013), honeybees (Apidae, *Apis mellifera*) (228), bumblebees (Apidae, *Bombus sp.*) (169) and other non-syrphid Diptera (243). The most abundant insect groups in 2015 remained the same, but there was a notable shift in abundances from flies towards bees: hoverflies (617), honeybees (704), bumblebees (624) and other non-syrphid Diptera (170). Extrapolated insect visitor species richness was unaffected by treatment (Table 3.1). Flower-visitor abundance was also unaffected by treatment (Table 3.1), but there was a significant effect of year ($F=16.107$, $p<0.001$) and a significant treatment:year interaction ($F=2.992$, $p=0.042$); the first growing season appeared to have fewer visitors in both heated treatments relative to CONTROL, while the second growing season results showed no such pattern (Figure 3.3 and Table 3.S2 in appendix 3.6.2). The frequency of visits per flower for all species combined and for just *G. segetum* (the species with highest floral abundance in both years) were significantly affected by treatment (all species: $\chi^2=2.104$, $p<0.001$, *G. segetum*: $\chi^2=15.420$, $p=0.002$), with higher values recorded from both heated treatments relative to the unheated ones (Figure 3.4 and Table 3.S4), but there was no significant effect of year (Tables 3.1 and 3.S4). The frequency of visits to *C. cyanus* flowers was unaffected by treatment or year (Table 3.S4). Mean diet breadth of visitors was unaffected by treatment (Table 3.S4) but there was a significant effect of year ($\chi^2=0.150$, $p<0.001$).

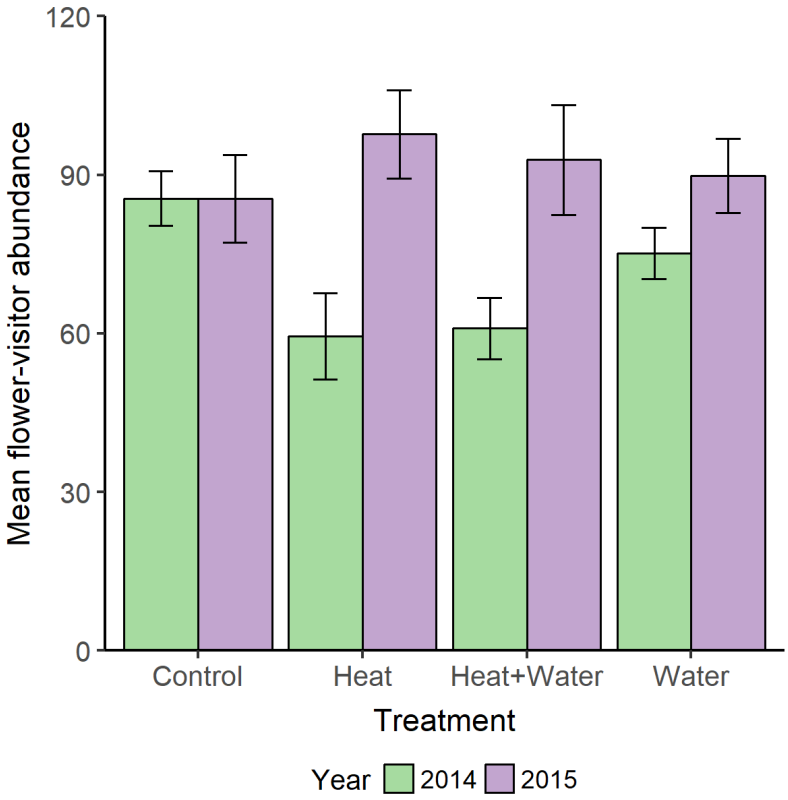


Figure 3.3 Mean flower-visitor abundance for each treatment in both sampling years, with standard error bars.

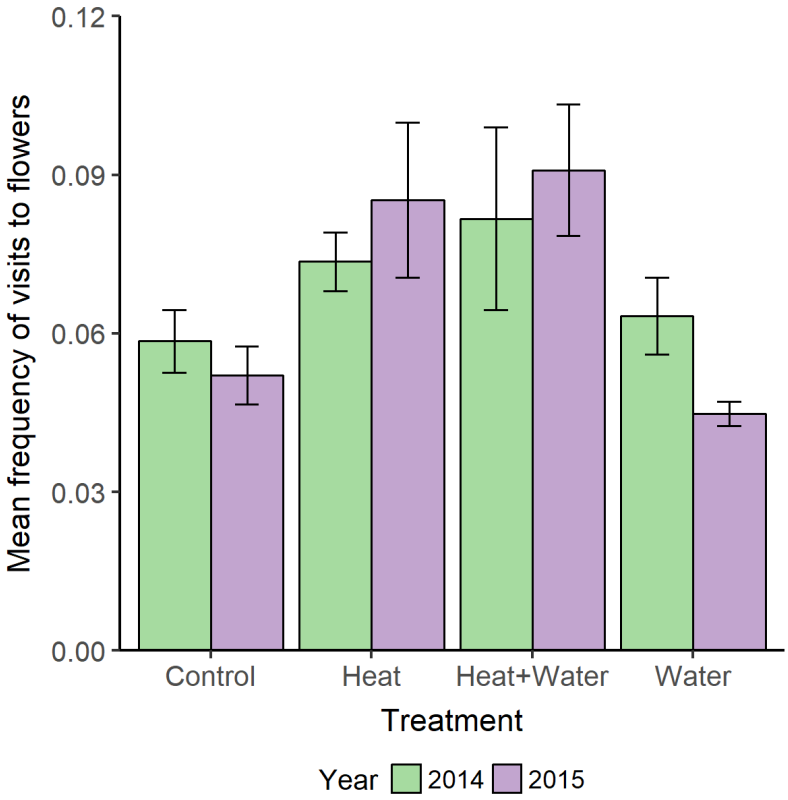


Figure 3.4 Mean frequency of visits per flower for each treatment in both sampling years, with standard error bars.

3.3.3 Objective 3: Investigating the impact of simulated warming on networks

Weighted connectance was significantly increased under simulated warming (χ^2=13.118, p=0.004) and there was also a significant effect of year (χ^2=18.625, p<0.001) as overall the values were higher in the second year (Table 3.S3 in appendix 3.6.2). Interaction evenness was also significantly increased under simulated warming (χ^2=9.743, p=0.021), but was unaffected by year (Table 3.2). However, after applying a Bonferroni correction, interaction evenness was no longer found to be significantly affected by treatment (Table 3.2). Generality was unaffected by treatment (Table 3.2) but there was a significant effect of year (F=12.481, p<0.001) as the values were higher in the first year (see Table 3.S3). Vulnerability was unaffected by treatment and year (Table 3.2). The structure of the networks appears consistent across treatments, but very different between years (Figure 3.5).

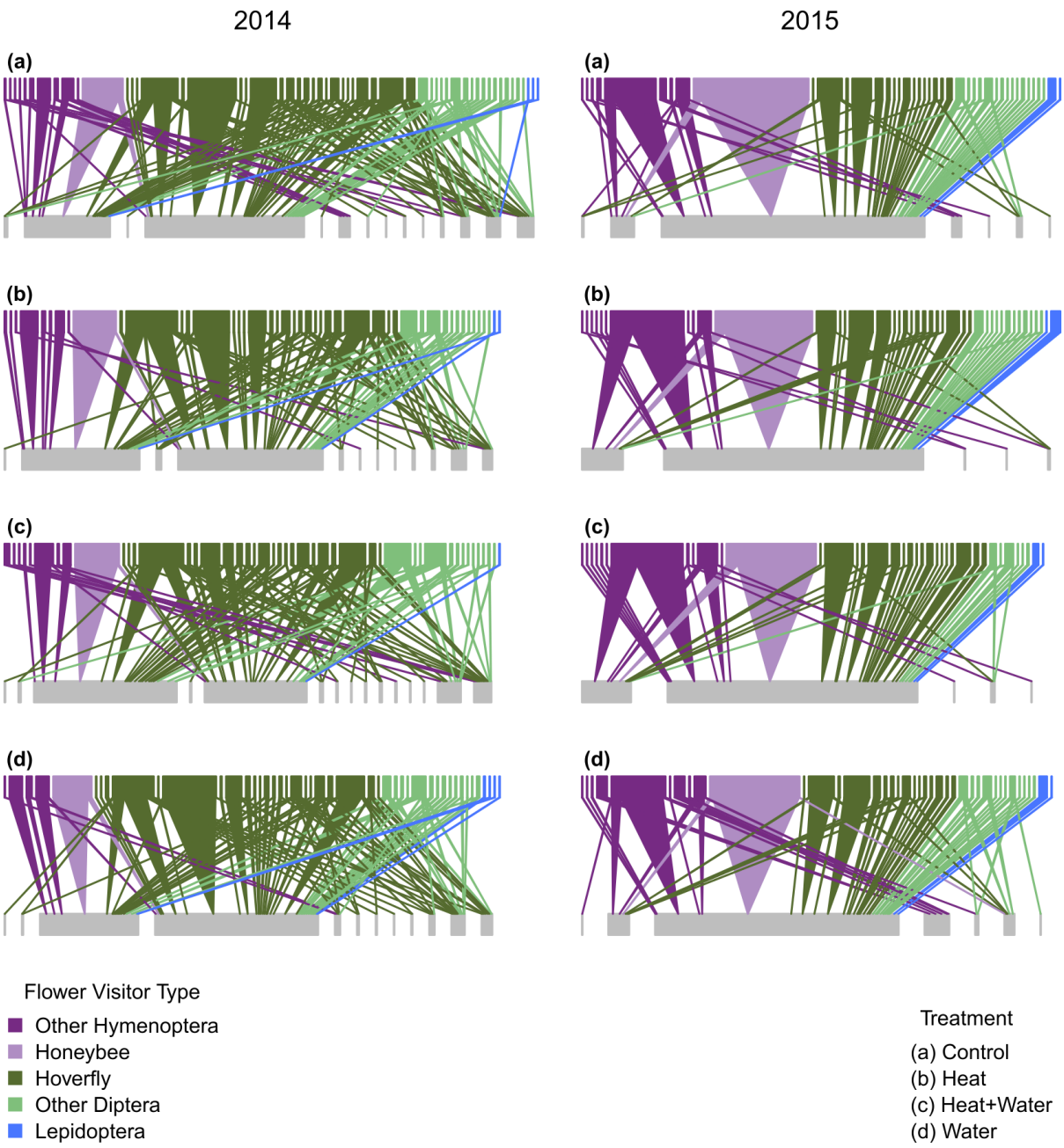


Figure 3.5 Species interaction networks for each treatment in both sampling years, showing the different flower visitor types. Width of species rectangles represents total number of interactions that species made and width of connections between the trophic levels represents the frequency of that particular plant-insect interaction pairing.

Variable	Treatment	Mean	Effect Size	Treatment P	Year P	Interaction P
Weighted	Control	0.1675 ± 0.0121	-2.0590 ± 0.1183	*0.004*	*<0.001*	0.390
Connectance	Heat	0.2052 ± 0.0166	0.2340 ± 0.0902			
	Heat+Water	0.2131 ± 0.0125	0.2974 ± 0.0895			
	Water	0.1750 ± 0.0070	0.0562 ± 0.0925			
Generality	Control	1.4110 ± 0.0732	1.7626 ± 0.1196	0.974	*0.001*	0.800
	Heat	1.4343 ± 0.0833	0.0233 ± 0.0938			
	Heat+Water	1.4444 ± 0.0730	0.0334 ± 0.0938			
	Water	1.4527 ± 0.0677	0.0417 ± 0.0938			
Vulnerability	Control	7.1448 ± 0.4275	6.5765 ± 0.7722	0.883	0.382	0.841
	Heat	7.5470 ± 0.4358	0.4021 ± 0.6058			
	Heat+Water	7.5686 ± 0.4996	0.4237 ± 0.6058			
	Water	7.5102 ± 0.3286	0.3653 ± 0.6058			
Interaction	Control	0.5870 ± 0.0203	0.4930 ± 0.1327	*0.021**	0.206	0.168
Evenness	Heat	0.6531 ± 0.0234	0.2931 ± 0.1045			
	Heat+Water	0.6459 ± 0.0148	0.2488 ± 0.1042			
	Water	0.6055 ± 0.0110	0.0715 ± 0.1030			

* Non-significant at Bonferroni corrected alpha of 0.0125

Table 3.2 Effects of treatments on network descriptors for both years combined. Mean values are of the raw data. Effect sizes and P values of Treatment and Year are taken from models without the interaction term, effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

3.3.4 Objective 4: Evaluating the effects of simulated warming on wildflower seed set

All species of wildflower showed significant effects of treatment on either seed number per seed head (*C. cyanus, S. media, V. persica*), average seed weight (*L. purpureum*), or both (*G. segetum*) (Table 3.3). *C. cyanus* seed number was lower in the two heated treatments than in the two unheated ones in both years; this was highly significant in 2014 (χ^2=20.089, p<0.001) but non-significant in 2015 (χ^2=6.331, p=0.097), most likely due to the smaller sample size. *C. cyanus* average seed weight was not significantly affected by treatment in either year (Table 3.3). *G. segetum* showed a consistent pattern of simulated warming reducing both seed number and seed weight in 2014 and 2015 (Table 3.3). This effect was significant for seed number in both years (2014: χ^2=13.005, p=0.005; 2015: χ^2=19.817, p<0.001), and for seed weight in 2015 (χ^2=12.026, p=0.007). Simulated warming significantly reduced *L. purpureum* seed weight (χ^2=15.962, p=0.001). *S. media* seed number was significantly reduced by simulated warming (χ^2=21.777, p<0.001) but seed weight was unaffected (Table 3.3). *V. persica* was the only species to respond positively to the increase in temperature; both seed number and seed weight were higher under simulated warming and this effect was highly significant for seed number (χ^2=22.269, p<0.001), but non-significant for seed weight (Table 3.3).

		2014			2015		
Variable	**Treatment**	**Mean**	**Effect Size**	**P value**	**Mean**	**Effect Size**	**P value**
C. cyanus	Control	24.0333 ± 0.6495	24.0333 ± 0.7502	*<0.001*	22.7857 ± 1.8283	22.7120 ± 1.9730	0.097
Seed Number	Heat	19.7667 ± 0.7712	-4.2667 ± 1.0610		19.2143 ± 0.9089	-3.4800 ± 2.8020	
	Heat+Water	20.4667 ± 0.7010	-3.5667 ± 1.0610		17.6667 ± 2.0087	-5.0450 ± 2.7600	
	Water	23.6333 ± 0.8623	-0.4000 ± 1.0610		23.7500 ± 2.6490	1.0380 ± 2.9230	
C. cyanus	Control	3.9131 ± 0.2046	3.9131 ± 0.1998	0.055	3.3440 ± 0.2736	0.1023 ± 0.0276	0.664
Seed Weight	Heat	4.2359 ± 0.1443	0.3227 ± 0.2826		3.6848 ± 0.3202	0.0041 ± 0.0414	
	Heat+Water	3.9747 ± 0.1679	0.0616 ± 0.2826		3.0714 ± 0.2660	0.0349 ± 0.0349	
	Water	3.4758 ± 0.1789	-0.4374 ± 0.2826		2.6383 ± 0.0952	0.0473 ± 0.0424	
G. segetum	Control	285.5556 ± 10.7561	285.5560 ± 16.2980	*0.005*	281.3889 ± 11.9205	281.3890 ± 10.0000	*<0.001*
Seed Number	Heat	220.0000 ± 15.9136	-65.5560 ± 23.0490		241.1111 ± 8.1449	-40.2780 ± 14.1420	
	Heat+Water	220.4667 ± 12.4410	-65.0890 ± 24.1740		227.6111 ± 10.4688	-53.7780 ± 14.1420	
	Water	281.3889 ± 8.9399	-4.1670 ± 23.0490		285.5556 ± 9.0540	4.1670 ± 14.1420	
G. segetum	Control	1.5491 ± 0.0928	0.5060 ± 0.1307	0.094	1.6611 ± 0.0969	1.6611 ± 0.0935	*0.007*
Seed Weight	Heat	1.2825 ± 0.0947	0.1889 ± 0.1769		1.3015 ± 0.0663	-0.3596 ± 0.1323	
	Heat+Water	1.1189 ± 0.0857	0.4189 ± 0.1866		1.2559 ± 0.0755	-0.4052 ± 0.1323	
	Water	1.5605 ± 0.0757	-0.0325 ± 0.1823		1.5488 ± 0.0553	-0.1122 ± 0.1323	

Table 3.3 Effect of treatment on wildflower seed set and weight for both field seasons separately. Mean values are of the raw data. Effect sizes are taken from the models, effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

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		2014			2015		
Variable	**Treatment**	**Mean**	**Effect Size**	**P value**	**Mean**	**Effect Size**	**P value**
L. purpureum	Control	- -	- -	-	0.8117 ± 0.0340	0.8117 ± 0.0465	*0.001*
Seed Weight	Heat	- -	- -		0.6830 ± 0.0407	-0.1247 ± 0.0669	
	Heat+Water	- -	- -		0.6873 ± 0.0482	-0.1231 ± 0.0700	
	Water	- -	- -		0.9423 ± 0.0331	0.1306 ± 0.0658	
V. persica	Control	- -	- -	-	11.4333 ± 0.9811	11.4333 ± 0.8941	*<0.001*
Seed Number	Heat	- -	- -		16.4828 ± 0.8576	5.0517 ± 1.2750	
	Heat+Water	- -	- -		15.3000 ± 0.8725	3.8667 ± 1.2645	
	Water	- -	- -		10.6000 ± 0.8089	-0.8333 ± 1.2645	
V. persica	Control	- -	- -	-	0.3831 ± 0.0498	2.9068 ± 0.4346	0.057
Seed Weight	Heat	- -	- -		0.7442 ± 0.1544	-1.2320 ± 0.5677	
	Heat+Water	- -	- -		0.6108 ± 0.0602	-1.0864 ± 0.5645	
	Water	- -	- -		0.3869 ± 0.0761	-0.0193 ± 0.5832	
S. media Seed	Control	- -	- -	-	13.8333 ± 0.4397	13.8333 ± 0.7398	*<0.001*
Number	Heat	- -	- -		10.2963 ± 0.7276	-3.4479 ± 1.0607	
	Heat+Water	- -	- -		11.6667 ± 0.6667	-2.1667 ± 1.0462	
	Water	- -	- -		15.7333 ± 0.3649	1.9000 ± 1.0462	
S. media Seed	Control	- -	- -	-	0.3802 ± 0.0198	0.3802 ± 0.0262	0.876
Weight	Heat	- -	- -		0.3976 ± 0.0182	0.0171 ± 0.0377	
	Heat+Water	- -	- -		0.4074 ± 0.0260	0.0272 ± 0.0371	
	Water				0.0272 ± 0.0293	0.0094 ± 0.0371	

Table 3.3 Effect of treatment on wildflower seed set and weight for both field seasons separately. Mean values are of the raw data. Effect sizes are taken from the models, effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

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3.4 Discussion

This experiment has yielded the first field-based empirical evidence of simulated climate-warming impacting arable wildflowers and their interactions with insect pollinators. We found that a moderate increase in temperature of 1.5 °C caused a significant reduction in the number of flowers and also negatively affected nectar production of some common non-crop plants. The insect pollinators were not directly affected by the experimental treatments in terms of species richness, but the abundance of visitors was reduced in one year and the frequency of visits to individual flowers was increased in both. The increase in temperature also lead to an increase in plant-flower visitor network complexity, while consumer-resource asymmetries and structural evenness were unaffected. All but one of the wildflower species examined was negatively affected in terms of seed production (i.e. seed number and/or seed weight), whereas *V. persica* produced more seeds in the heated treatments.

3.4.1 Limitations

There are several main limitations to this study. Firstly, the small scale of the experiment makes it challenging to scale-up findings to impacts on landscape ecosystem processes. Other studies that have looked at experimental climate warming in situ have used the same or similar setup as it is currently the most appropriate and economically viable method (Berthe et al., 2015; Kimball, 2005; Rollinson and Kaye, 2012). Future experimental warming studies will need to be replicated spatially in a wide range of habitats and coordinated in such a way to improve meta-analyses. Secondly, the small scale of the experimental plots also increases the potential for edge effects. Once again this points to a need for larger-scale studies, both in terms of replicate size as well as number. While the setup used in this and other studies for simulated warming experiments restrict the plot size to 2 x 2m, there have been more recent heating array demonstrations that allow for greater scales, though at a greater cost (Kimball et al., 2008). Thirdly, the open-air nature of the experiment allowed free movement of insects in and out of the plots, preventing direct manipulation of them with the experimental treatments. Given the aims of this study to investigate the responses of whole communities of wild organisms in situ, to achieve this would either involve a prohibitive spatial scale (due to the foraging distances of flower visiting insects) or an enclosed setup that would constrain natural insect behaviour and

exclude many species. As a result, our experiment took a bottom-up approach, whereby we manipulated the plants directly and examined how the foraging behaviour of the insect community responded to any changes in the wildflowers, rather than inferring direct impacts upon the insects. Finally, for logistical and financial reasons we were unable to examine the impacts of elevated CO_2 concentration. It is well documented that increasing CO_2 concentrations in situ can lead to increased plant productivity and seed set/weight (Ainsworth and Long, 2005), and there is some evidence for elevated CO_2 directly affecting the abundance of certain insect groups from open air field experiments (Facey et al., 2017). Thus, simulating increases in CO_2, temperature and precipitation in a fully factorial experiment, with sufficient replicates for statistical power, is a research priority.

3.4.2 Objective 1: Investigating the effects of simulated warming on wildflower floral resources

The composition of the floral community was unaffected by the experimental treatments. This is not an unexpected result as the whole experimental area was ploughed before the start of the experiment each year. This also explains why there was no significant difference in the flowering plant species richness between the treatments. Most simulated warming experiments examining vegetation communities are conducted in semi-natural habitats of predominantly perennial species and are run continuously for several years. Studies conducted in sub-alpine and tundra habitats have shown that it can take several years of continuous warming for any changes in vegetation community and species richness to be found (Klein et al., 2004; Walker et al., 2006), while experiments in warmer habitats have found no changes even after several years (Peñuelas et al., 2007; Price and Waser, 2000). It is very likely that the time-frame of the system we used, an annual system that is cut and re-sown every year, is too short to be able to show such floral community changes and any treatment effects are instead likely to be found at the level of the individual organisms for each species, in each year.

The significant difference in floral abundance is a very striking result that has obvious implications not only for the possible future plant communities via a reduction in fecundity, but also for flower-visiting insects. Our experiment showed that under an increase of 1.5 °C there was almost a 40% reduction in floral units throughout the season; this represents a significant decrease in available food for flower visitors. It is also worth noting that the addition of extra water had no ameliorative effects upon this decrease in floral abundance.

To date, most of the research that has looked at flowering responses to climate change comes from tundra and montane habitats and looks at changes in flowering periods rather than flower abundances, but there is limited evidence from both simulated warming experiments and a long-term passive project that climate warming can cause a reduction in the numbers of flowering plant individuals (Liu et al., 2012; Saavedra et al., 2003), flowers per plant (Saavedra et al., 2003) and flower size (Hoover et al., 2012) for a variety of species (see Table 3.S5 in appendix 3.6.2 for results on reduced flower size for *G. segetum* from this study). In addition to a reduction in flowers, the simulated heating also caused a reduction in nectar volumes; each of the three species responded differently (particularly with respect to the addition of water in combination with heating, see Figure 3.2), but in all cases the heated treatments produced less nectar than the unheated ones, and for two of the species (*L. Purpureum* and *V. persica*) the reduction was highly significant and very marked. Very few studies have investigated the impacts of climate change on nectar resources, but research from laboratory controlled-temperature experiments has found evidence for increased nectar volumes and sugar concentrations under increased temperatures (Petanidou and Smets, 1996) and under static vs. fluctuating temperatures (Walker et al., 1974). Our results appear to run contrary to these findings, but the difference could potentially be explained by the manner and situation of the heating, as our plants were growing naturally in situ and heated from above; perhaps the nectar reductions we recorded were caused by increased evaporation, or maybe the more realistic field setting produced more field-realistic results. Or it could simply be that the plant species we used respond to temperature differently than others that have previously been studied (there is evidence for variation between species, see Petanidou and Smets (1996)). Regardless of why our results show a reduction in nectar volumes under the heated treatments, the fact that they do represents a further reduction in food for flower-visiting insects.

3.4.3 Objective 2: Assessing the effects of simulated warming on visitation

The composition of the insect community was significantly different between treatments in 2014 but not in 2015; this could be due to the overall change in the community between the two years. Hoverflies dominated the community in 2014, whereas honeybees and bumblebees dominated in 2015. The difference in community response to the treatments could be driven by differences in reproductive and foraging behaviours. Adult

bees feed their offspring and so have to make foraging trips before returning to their nest/colony, whereas hoverflies are much less spatially restricted as they do not need to return to an area after oviposition, which potentially makes them free to spend more time in their optimal foraging habitats. It is also far more likely that our experimental plots would represent a suitable oviposition site for hoverflies (those with insectivorous larvae) than they would be suitable nesting sites for bumblebees or honeybees. Indeed, during plot observations it was noted that in 2014 there were many hoverflies setting up breeding territories and mating within the plots, whereas in 2015 there were far fewer observations of hoverfly breeding behaviour, while only two bee nesting sites were observed in the experimental area (one in each year) and both of those were a solitary bee. To be able to fully capture the life histories of free-moving flower visitors would require a far greater scale than was used in this experiment, until that scale is achieved, such manipulations can only be indirect with respect to the insect visitors.

Visitor species richness and abundance were unaffected by treatment when both years of data are combined; this suggests that overall, the treatments were not affecting the whole community of insect flower visitors directly. Recent research has shown that higher temperatures can lead to lower bee species diversity (Papanikolaou et al., 2016), but our findings make sense within the context of our experiment as it was a small scale, with close proximity of experimental plots, and lacked any barriers to insect movement. However, there was a significant effect of year and a significant treatment:year interaction on visitor abundance; in 2014 the abundance was notably lower in the two heated treatments, while in 2015 it was slightly higher (Figure 3.3, and Table 3.S2 in appendix 3.6.2). This again could be due to the change in dominant insect group, with the hoverflies responding to the simulated warming more strongly than the honeybees and bumblebees and showing a preference for foraging in the unheated plots, which had more flowers, while this effect appears to have been masked in the second year by the greater abundance of bees. Once again, the different responses of the two insect groups are likely driven by the different foraging requirements of their respective reproductive strategies. The addition of water had no ameliorative effect on the reduction in visitor abundance in 2014, though this is to be expected if floral abundance is driving this difference. Currently, there are very few published papers which have looked at simulated climate warming and free-ranging insect responses. Berthe et al. (2015) used the same experimental set up as this research to

investigate the impacts of simulated warming on beetles; they found that warming resulted in lower diversity indices, but that this was caused by higher activity-densities of the four most-trapped species in the heated plots, and they also found differing responses by family.

Some more clear-cut findings are that the frequency of visits to individual flowers of all species combined, and to those of just *G. segetum* (Table 3.S4), were significantly affected by treatment, with higher values found in the heated treatments. This is a logical result as there were drastically fewer flowers in the heated plots versus the unheated ones, but due to the small scale of the experiment and proximity of the plots, broadly speaking, the same community of insects was visiting all the plots in the experiment. It is unclear why the frequency of visits to *C. cyanus* was unaffected by treatment, but it may relate to the behaviour of the insects that preferred to visit it, which in this experiment was predominantly bees (67.2%, only 41.0% of visits to *G. segetum* were bees). Bees are unlikely to visit a flower that has recently been visited due to the chemical cues left behind by previous visitors (Williams, 1998).

3.4.4 Objective 3: Investigating the impact of simulated warming on networks

There was no effect of treatment on generality or vulnerability, but this is perhaps unsurprising given that we found no differences in species richness for either plants or insects as a result of the treatments. Generality was significantly affected by year and was lower in 2015 (Table 3.S3 in appendix 3.6.2), which can be explained by the lower number of flower species that were recorded in 2015. The significant effect of year upon weighted connectance is most likely caused by the difference in flower species richness between years; weighted connectance was higher in 2015 (Table 3.S3) when there were fewer flower species present in the plots but the same number of insect species, which makes it more likely that more of the potential interactions were recorded.

The increased weighted connectance found in the heated treatments means that the insects are visiting a greater proportion of the different flower species present in those plots than in the unheated ones. There is also a trend for higher interaction evenness in the heated treatments. These findings could be explained by the reduction in floral abundance and/or nectar volumes in the heated plots causing species to broaden their diets in search of sufficient food. They could also be explained by a reduction in flower species richness which

would increase the chance of detecting more of the possible interactions and could affect interaction evenness. However, we examined diet breadth (see Table 3.S4) and flower species richness (Table 3.1) and found no significant effect of treatment on either, but there is a trend for both variables; they are both lower in the heated treatments. This illustrates the value of using a network approach; if we only looked at these and other variables in isolation then we would miss the cumulative effect of them all combined. It is likely that the changes in connectance and interaction evenness are caused by the accruing impact of small changes in many aspects of the whole community.

Our findings indicate that plant-flower-visitor network structure is robust to changes in temperature, which supports the conclusions of other researchers who have investigated this topic. Hegland et al. (2009) reviewed the evidence for climate warming impacts on plant-pollinator interactions and found that these networks are robust to changes in climate due to their nested and asymmetric structure and dynamic nature. However, more recent research by Burkle et al. (2013) found changes in plant-pollinator network structure as a result of climate warming; they found nestedness decreased as a result of loss of species and diet breadth shift. This indicates that a greater disturbance to the networks than was caused by our experiment is necessary to elicit changes in structure, though this is certainly likely under an increase in temperature that is universal rather than just in 12 2x2m foraging patches. A more alarming finding is that a significant increase in network complexity was found as a result of increased temperature, despite the limitations of our experiment. This suggests that these networks are potentially very sensitive to climate change through the cumulative impact that it has on features such as floral abundance, nectar volumes, species richness, and subsequent changes in visitor foraging behaviour.

3.4.5 Objective 4: Evaluating the effects of simulated warming on wildflower seed set

All five species of wildflower that were examined for an effect of treatment on seed set and weight showed a significant response. Four of the species responded negatively to the increase in temperature, by producing either fewer (*C. cyanus* and *S. media*) or lighter seeds (*L. purpureum*), or both (*G. segetum*) (Table 3.3). These negative responses to the temperature increase were consistent even when additional water was applied to the plants and were consistent across both years for the species sampled in both seasons (though this was not significant for *C. cyanus* in 2015). The final wildflower species, *V. persica*, responded

positively to the increase in temperature both in terms of seed set and average seed weight, though the latter was not significant. This highlights the complexity of a community-wide response to simulated warming and demonstrates that there will be winners and losers in any environment. The potential implications are that the plant community could change over time, as species like *S. media* lose out to species like *V. persica*, which are better able to adapt to and capitalise on the new environmental conditions.

There is very little information in the literature on how wildflower seed set is directly affected by climate change as most studies have looked at crop plants; there is evidence for negative effects of increasing temperature on seed set and yield for a range of species such as wheat (Asseng et al., 2004; Liu et al., 2016), kidney beans (Prasad et al., 2002), and sorghum (Prasad et al., 2006). Jin et al. (2011) looked at how a range of vegetative variables as well as seed weight of thale cress (*Arabidopsis thaliana*) responded to changes in temperature and found that moderate increases in temperature positively affected seed weight, similarly to our findings with *V. persica*, but at higher temperatures the impact was negative. Both *A. thaliana* and *V. persica* are common generalist weeds in the UK (Rose and O'Reilly, 2006), able to flourish in a variety of habitats and have also thrived when introduced outside of their native range. This adaptable and resilient nature is perhaps why both species are able to cope well under small increases of temperature. In contrast, wild *G. segetum* and *C. cyanus* are both very rare and declining in the UK and across Europe and are restricted to arable land (Rose and O'Reilly, 2006; Sutcliffe and Kay, 2000). These two cornfield annuals have been threatened by agricultural intensification as they prefer a within-crop habitat where they are seen as weeds detrimental to cereal harvests. Our findings suggest that these rare plants are also threatened by climate change as the increase in temperature directly reduced seed set for both species and seed weight for *G. segetum*, which has obvious implications for seedling recruitment and long-term population viability. As previously discussed, we were unable to simulate projected increases in CO_2 in our study, but it is another factor that needs to be considered; increased CO_2 concentrations will allow greater plant productivity and could increase seed production (Ainsworth and Long, 2005), although this effect may not be able to fully offset the losses due to temperature increases (Long et al., 2006).

What is particularly interesting about these results, is that the increased frequency of visits to flowers did not seem to have any beneficial effect on the seed set or seed weight of

the flowers that were negatively affected by the treatment. We know that increased visitation can be beneficial for many plants and is linked to increased seed set for some species (Garibaldi et al., 2013; Garratt et al., 2014b). There is also evidence of insect pollinators recovering yield after heat stress (Bishop et al., 2016). However, there are also plenty of examples in the literature showing that this relationship is not quite so straight forward, because both insect type and pollinator dependence can be crucial factors in determining how beneficial an insect's visits to a flower are (Franzén and Larsson, 2009; Garratt et al., 2016; Lundgren et al., 2013). It seems more likely here, that the direct impact of the raised temperature on seed development is having a greater overall effect on seed set and weight than the increased frequency of visits. This is potentially very detrimental for some insect-pollinated plants, such as *G. segetum*, as it suggests that climate warming will have negative impacts on their reproduction even if pollinator visitation is increased.

In conclusion, our study demonstrates the negative consequences that climate-warming might have on flower visiting insects and wildflowers in arable farming systems, but it also highlights the need for larger-scale, replicated simulated warming experiments, and for more field studies considering how climate change may affect species interactions, flowering, and seed set of wildflowers. The considerable inter-annual variation found in the plant and insect communities here also demonstrates the need for longer-term investigations and for greater temporal consideration. We have shown that a relatively small increase in temperature can have very large effects upon floral resources, wildflower reproduction and interaction network complexity, and that such impacts are not offset when water is increased. Our findings also highlight that different species respond to changing climatic conditions very differently, with one species of common generalist weed thriving, while two rare and endangered specialist cornfield annuals failed to reproduce as effectively, and in the case of one of them this is despite increased visitations. We simulated representative increases in temperature and precipitation, but not CO2, which is an extremely important factor that should also be included in future field experiments, although the set-up costs are likely to be high. The focus for climate change research in agricultural landscapes is understandably on yields and food security, but it needs to expand to incorporate the wider range of direct and indirect interactions provided by biodiversity, including ecosystem services such as insect pollination.

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3.6 Appendix

3.6.1 Methods

Family	Common Name	Scientific Name	Sowing weight per plot (g)
Apiaceae	Upright Hedge Parsley	*Torilis japonica*	2
Asteraceae	Cornflower	*Centaurea cyanus*	0.6
Asteraceae	Corn Marigold	*Glebionis segetum*	0.8
Caryophyllaceae	Corncockle	*Agrostemma githago*	0.2
Fabaceae	Common Vetch	*Vicia sativa*	0.4
Laminaceae	Red deadnettle	*Lamium purpureum*	0.4
Papaveraceae	Common Poppy	*Papaver rhoeas*	0.4
Ranunculaceae	Corn Buttercup	*Ranunculus arvensis*	0.4

Table 3.S1 Wildflower species and sowing weights

All wildflower seeds were purchased from Emorsgate Seeds (http://wildseed.co.uk/home). Wheat was sown on 15/04/14 in the first field season, and wildflowers on 16/04/14. In the second field season wheat was sown on 14/04/15 and wildflowers on 15/04/15.

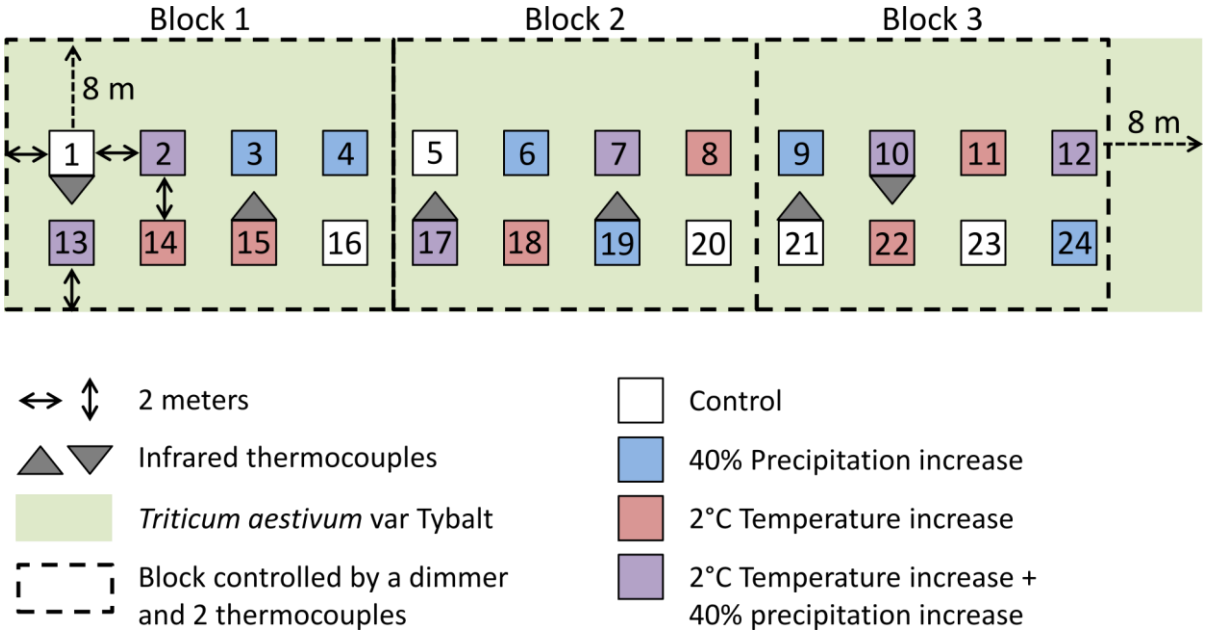

Figure 3.S1 Simulated warming experiment layout and design.

3.6.2 Results

		2014	2015
Variable	**Treatment**	**Mean**	**Mean**
Visitor abundance	Control	85.5000 ± 5.1559	85.5000 ± 8.2452
	Heat	59.5000 ± 8.1925	97.6667 ± 8.3533
	Heat+Water	61.0000 ± 5.8023	92.8333 ± 10.3776
	Water	75.1667 ± 4.8471	89.8333 ± 7.0020
Visitor richness (extrapolated)	Control	36.1056 ± 3.5099	36.1514 ± 8.7643
	Heat	42.8869 ± 6.6308	31.0238 ± 6.6619
	Heat+Water	30.8531 ± 5.3439	40.6012 ± 11.3870
	Water	40.1347 ± 3.6521	45.0351 ± 11.9215
Visits per flower (all species combined)	Control	0.0585 ± 0.0059	0.0521 ± 0.0055
	Heat	0.0736 ± 0.0056	0.0853 ± 0.0147
	Heat+Water	0.0817 ± 0.0172	0.0909 ± 0.0124
	Water	0.0633 ± 0.0073	0.0448 ± 0.0023
Visits per *C.cyanus* flower	Control	0.1215 ± 0.0249	0.2771 ± 0.0999
	Heat	0.1683 ± 0.0177	0.1636 ± 0.0472
	Heat+Water	0.2272 ± 0.0465	0.2333 ± 0.0665
	Water	0.1384 ± 0.0214	0.1594 ± 0.0516
C.cyanus floral abundance	Control	230.3333 ± 39.9430	19.3333 ± 8.8644
	Heat	144.8333 ± 16.4609	70.0000 ± 26.5393
	Heat+Water	127.1667 ± 21.1871	60.0000 ± 26.5544
	Water	181.3333 ± 18.6273	30.6667 ± 11.3363
Visits per *G. segetum* flower	Control	0.0921 ± 0.0179	0.0955 ± 0.0118
	Heat	0.1522 ± 0.0178	0.1048 ± 0.0136
	Heat+Water	0.1564 ± 0.0282	0.1250 ± 0.0143
	Water	0.0845 ± 0.0051	0.0980 ± 0.0138
G. segetum floral abundance	Control	569.3333 ± 98.7481	844.3333 ± 136.5884
	Heat	208.8333 ± 58.4861	845.1667 ± 88.3566
	Heat+Water	172.8333 ± 85.2926	701.6667 ± 192.0609
	Water	474.6667 ± 51.2859	805.5000 ± 115.7295
Diet breadth	Control	1.3903 ± 0.0660	1.2165 ± 0.0489
	Heat	1.3165 ± 0.0566	1.1389 ± 0.0512
	Heat+Water	1.3616 ± 0.0822	1.2536 ± 0.0663
	Water	1.4436 ± 0.0331	1.2436 ± 0.0761

Table 3.S2 Means of visitor and flower data for each treatment, for both years separately. Mean values are of the raw data and given ± their standard errors.

		2014	2015
Variable	**Treatment**	**Mean**	**Mean**
Weighted connectance	Control	0.1388 ± 0.0089	0.1962 ± 0.0153
	Heat	0.1812 ± 0.0204	0.2292 ± 0.0239
	Heat+Water	0.1821 ± 0.0141	0.2441 ± 0.0100
	Water	0.1657 ± 0.0068	0.1843 ± 0.0116
Generality	Control	1.5305 ± 0.0957	1.2915 ± 0.0934
	Heat	1.5643 ± 0.1182	1.3042 ± 0.0988
	Heat+Water	1.5073 ± 0.0963	1.3815 ± 0.1123
	Water	1.6091 ± 0.0429	1.2964 ± 0.0924
Vulnerability	Control	7.1595 ± 0.4358	7.1302 ± 0.7836
	Heat	7.1927 ± 0.5653	7.9013 ± 0.6827
	Heat+Water	7.1453 ± 0.5898	7.9919 ± 0.8239
	Water	7.5156 ± 0.5488	7.5048 ± 0.4170
Interaction Evenness	Control	0.6120 ± 0.0182	0.5619 ± 0.0351
	Heat	0.6680 ± 0.0281	0.6382 ± 0.0391
	Heat+Water	0.6261 ± 0.0114	0.6656 ± 0.0260
	Water	0.6334 ± 0.0107	0.5776 ± 0.0102

Table 3.S3 Means of network descriptors for each treatment, for both years separately. Mean values are of the raw data and given ± their standard errors.

Variable	Treatment	Mean	Effect Size	Treatment P	Year P	Interaction P
Diet breadth	Control	1.3034 ± 0.0471	0.3674 ± 0.0683	0.267	*<0.001*	0.867
	Heat	1.2277 ± 0.0452	0.0740 ± 0.0577			
	Heat+Water	1.3076 ± 0.0529	-0.0037 ± 0.0549			
	Water	1.3436 ± 0.0498	-0.0343 ± 0.0538			
Visits per *C. cyanus* flower	Control	0.1922 ± 0.0508	0.1275 ± 0.0627	0.399	0.218	0.356
	Heat	0.1662 ± 0.0222	-0.0260 ± 0.0501			
	Heat+Water	0.2300 ± 0.0373	0.0377 ± 0.0501			
	Water	0.1479 ± 0.0249	-0.0443 ± 0.0501			
Visits per *G. segetum* flower	Control	0.0938 ± 0.0102	85.1600 ± 29.7400	*0.002*	0.192	0.357
	Heat	0.1285 ± 0.0129	-52.4500 ± 24.1800			
	Heat+Water	0.1407 ± 0.0158	-62.3000 ± 23.3600			
	Water	0.0912 ± 0.0073	6.5400 ± 29.6800			

Table 3.S4 Effects of treatments on insect visitor diet breadth and frequency of flower visits to *C. cyanus* and *G. segetum* for both years combined. Mean values are of the raw data. Effect sizes and P values of Treatment and Year are taken from models without the interaction term, effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

Variable	Treatment	Mean	Effect Size	Treatment P
C. cyanus nectar volume	Control	0.2095 ± 0.0307	0.7168 ± 0.0616	0.578
	Heat	0.1807 ± 0.0294	0.0109 ± 0.0864	
	Heat+Water	0.1401 ± 0.0323	0.0549 ± 0.0907	
	Water	0.2835 ± 0.0373	-0.0878 ± 0.0939	
L. purpureum nectar volume	Control	0.3758 ± 0.0399	2.6610 ± 0.3691	*<0.001*
	Heat	0.1032 ± 0.0389	7.0281 ± 2.1146	
	Heat+Water	0.2578 ± 0.0781	1.2181 ± 1.0025	
	Water	0.3472 ± 0.0327	0.2194 ± 0.5326	
V. persica nectar volume	Control	0.1426 ± 0.0168	0.1425 ± 0.0167	*<0.001*
	Heat	0.0504 ± 0.0093	-0.0928 ± 0.0253	
	Heat+Water	0.0337 ± 0.0066	-0.1088 ± 0.0250	
	Water	0.1269 ± 0.0167	-0.0136 ± 0.0237	
G. segetum flower disc diameter (mm)	Control	14.2450 ± 0.5010	14.2454 ± 0.4675	*0.014*
	Heat	13.0117 ± 0.3928	-1.2333 ± 0.6612	
	Heat+Water	13.2900 ± 0.3819	-0.9550 ± 0.6612	
	Water	15.1933 ± 0.5686	0.9483 ± 0.6612	

Table 3.S5 Effects of treatments on wildflower nectar volumes and flower size. Mean values are of the raw data. Effect sizes are taken from the models, effect sizes of Heat, Heat+Water and Water are relative to Control, which was the intercept in all the models. Mean values and effect sizes are given ± their standard errors. Significant P values ($p<0.05$) are italicised.

Diet breadth, visits per G. segetum flower and G. segetum flower disc diameter were analysed using GLMs with inverse Gaussian error, and visits per C. cyanus flower using a GLM with Gaussian error.

Frequency of visits to species other than C. cyanus and G. segetum could not be analysed due to insufficient visit data.

Flower disc diameter of G. segetum was measured in 2015. After it was determined that the nectaries of this species were too small to sample using the 0.5 microL microcapillary tubes we had available, it was decided to measure the diameter of the floral disc to gain a rough proxy of nectar available via the size of the flower head. The logic being that these are composite flower heads containing many tiny individual inflorescences, a smaller disc means fewer and/or smaller inflorescences and less total nectar per flower head. This data was averaged for each plot, then analysed using a GLM with Gaussian error.

3.6.3 Species Lists

Type	Species
Sown species	*Agrostemma githago*
Sown species	*Centaurea cyanus*
Sown species	*Glebionis segetum*
Sown species	*Lamium purpureum*
Sown species	*Papaver rhoeas*
Sown species	*Ranunculus arvensis*
Sown species	*Vicia sativa*
Non-sown species	*Capsella bursa-pastoris*
Non-sown species	*Chenopodium album*
Non-sown species	*Cirsium arvense*
Non-sown species	*Cirsium dissectum*
Non-sown species	*Fallopia convolvulus*
Non-sown species	*Geranium sp.*
Non-sown species	*Lamium amplexicaule*
Non-sown species	*Matricaria discoidea*
Non-sown species	*Persicaria maculosa*
Non-sown species	*Poaceae sp1*
Non-sown species	*Poaceae sp2*
Non-sown species	*Polygonum aviculare*
Non-sown species	*Senecio vulgaris*
Non-sown species	*Sisymbrium officinale*
Non-sown species	*Solanum sp.*
Non-sown species	*Sonchus arvensis*
Non-sown species	*Sonchus asper*
Non-sown species	*Sonchus oleraceus*
Non-sown species	*Spergula arvensis*
Non-sown species	*Stellaria media*
Non-sown species	*Tripleurospermum indorum*
Non-sown species	*Urtica urens*
Non-sown species	*Veronica persica*
Non-sown species	*Viola arvensis*

Table 3.S6 List of all plant species recorded in the warming experiment. Includes sown and non-sown species, and flowering and non-flowering species.

Type	Species	2014	2015
Bumblebee	*Bombus hortorum*	8	24
Bumblebee	*Bombus hypnorum*	0	1
Bumblebee	*Bombus lapidarius*	82	454
Bumblebee	*Bombus pascuorum*	20	33
Bumblebee	*Bombus pratorum*	2	8
Bumblebee	*Bombus terrestris/lucorum*	57	103
Honeybee	*Apis mellifera*	228	704
Solitary Bee	*Andrena bicolor*	2	3
Solitary Bee	*Andrena haemorrhoa*	0	2
Solitary Bee	*Andrena nigroaenea*	0	2
Solitary Bee	*Andrena nitida*	0	1
Solitary Bee	*Andrena semilaevis*	1	0
Solitary Bee	*Anthophora furcata*	0	1
Solitary Bee	*Colletes daviesanus*	6	0
Solitary Bee	*Halictus rubicundus*	4	5
Solitary Bee	*Halictus tumulorum*	1	0
Solitary Bee	*Hylaeus communis*	1	0
Solitary Bee	*Lasioglossum calceatum*	5	1
Solitary Bee	*Lasioglossum morio*	1	0
Solitary Bee	*Megachile centuncularis*	0	3
Solitary Bee	*Megachile sp.*	0	1
Solitary Bee	*Osmia sp.*	0	1
Parasitoid Wasp	*Diadromus collaris*	1	0
Social Wasp	*Dolichovespula sylvestris*	1	0
Solitary Wasp	*Passaloecus sp.*	0	1
Lepidoptera	*Aglais io*	0	1
Lepidoptera	*Aglais urticae*	3	54
Lepidoptera	*Aphantopus hyperantus*	0	1
Lepidoptera	*Autographa gamma*	0	1
Lepidoptera	*Inachis io*	2	0
Lepidoptera	*Maniola jurtina*	0	1
Lepidoptera	*Pieris napi*	1	0
Lepidoptera	*Pieris rapae*	3	0
Lepidoptera	*Thymelicus sylvestris*	2	0
Non-syrphid Diptera	*Anthomyiidae sp.*	74	53
Non-syrphid Diptera	*Bellardia vulgaris/viarum*	8	6
Non-syrphid Diptera	*Calliphora vicina*	1	0
Non-syrphid Diptera	*Calliphora vicini*	0	2
Non-syrphid Diptera	*Calliphora vomitoria*	3	5
Non-syrphid Diptera	*Ceonosia trigrina*	1	0

Table 3.S7 List of all insect flower-visitor species recorded in the warming experiment. Includes species type and recorded frequency for each species in each year.

Continued on next two pages

Type	Species	2014	2015
Non-syrphid Diptera	*Chrysops relictus*	1	0
Non-syrphid Diptera	*Coenosia pumila*	1	0
Non-syrphid Diptera	*Delia radicum*	0	4
Non-syrphid Diptera	*Drosophila sp.*	2	0
Non-syrphid Diptera	*Empididae sp.*	0	1
Non-syrphid Diptera	*Empis livida*	73	48
Non-syrphid Diptera	*Eriothrix rufomaculata*	17	3
Non-syrphid Diptera	*Lucilia ceasar*	4	4
Non-syrphid Diptera	*Lucilia illustris*	5	3
Non-syrphid Diptera	*Lucilia richardsii*	0	1
Non-syrphid Diptera	*Lucilia sericata*	9	4
Non-syrphid Diptera	*Lucilia silvarum*	5	21
Non-syrphid Diptera	*Meigenia mutabalis*	1	0
Non-syrphid Diptera	*Melinda viridicyanea*	6	1
Non-syrphid Diptera	*Muscidae sp.*	0	1
Non-syrphid Diptera	*Odontomyia angulata*	2	0
Non-syrphid Diptera	*Phaonia incarna*	1	1
Non-syrphid Diptera	*Phaonia sp.*	0	1
Non-syrphid Diptera	*Pollenia angustigena*	0	1
Non-syrphid Diptera	*Pollenia pallida*	5	1
Non-syrphid Diptera	*Pollenia pediculata*	5	6
Non-syrphid Diptera	*Sarcophaga sp.*	4	0
Non-syrphid Diptera	*Sarcophagini sp.*	10	3
Non-syrphid Diptera	*Siphona geniculata*	2	0
Non-syrphid Diptera	*Tachinidae sp.*	1	0
Syrphidae (hoverfly)	*Cheilosia bergenstammi*	1	0
Syrphidae (hoverfly)	*Cheilosia pagana*	3	0
Syrphidae (hoverfly)	*Cheilosia sp.*	2	1
Syrphidae (hoverfly)	*Cheilosia vernalis*	6	2
Syrphidae (hoverfly)	*Chrysotoxum bicinctum*	2	0
Syrphidae (hoverfly)	*Dasysyrphus albostriatus*	1	0
Syrphidae (hoverfly)	*Episyrphus balteatus*	235	174
Syrphidae (hoverfly)	*Eristalinus sepulchralis*	6	1
Syrphidae (hoverfly)	*Eristalis abusivus*	10	0
Syrphidae (hoverfly)	*Eristalis arbustorum*	224	11
Syrphidae (hoverfly)	*Eristalis interruptus*	5	0
Syrphidae (hoverfly)	*Eristalis pertinax*	1	0
Syrphidae (hoverfly)	*Eristalis similis*	2	0
Syrphidae (hoverfly)	*Eristalis sp.*	0	1
Syrphidae (hoverfly)	*Eristalis tenax*	97	157

Table 3.S7 List of all insect flower-visitor species recorded in the warming experiment. Includes species type and recorded frequency for each species in each year.

Continued from previous page, and on next page

Type	Species	2014	2015
Syrphidae (hoverfly)	*Eupeodes corollae*	19	62
Syrphidae (hoverfly)	*Eupeodes latifasciatus*	0	6
Syrphidae (hoverfly)	*Eupeodes lundbecki*	0	1
Syrphidae (hoverfly)	*Eupeodes luniger*	18	23
Syrphidae (hoverfly)	*Helophilus hybridus*	6	0
Syrphidae (hoverfly)	*Helophilus pendulus*	34	2
Syrphidae (hoverfly)	*Helophilus trivittatus*	7	0
Syrphidae (hoverfly)	*Melanostoma mellinum*	16	10
Syrphidae (hoverfly)	*Melanostoma scalare*	2	0
Syrphidae (hoverfly)	*Merodon equestris*	1	1
Syrphidae (hoverfly)	*Neoascia podagrica*	4	0
Syrphidae (hoverfly)	*Platycheirus albimanus*	47	38
Syrphidae (hoverfly)	*Platycheirus ambiguus*	0	1
Syrphidae (hoverfly)	*Platycheirus manicatus*	5	1
Syrphidae (hoverfly)	*Platycheirus occultus*	0	2
Syrphidae (hoverfly)	*Platycheirus scutatus s.l.*	1	0
Syrphidae (hoverfly)	*Scaeva pyrastri*	1	11
Syrphidae (hoverfly)	*Sphaerophoria interrupta*	2	0
Syrphidae (hoverfly)	*Sphaerophoria scripta*	47	8
Syrphidae (hoverfly)	*Sphaerophoria sp.*	24	6
Syrphidae (hoverfly)	*Syritta pipiens*	138	62
Syrphidae (hoverfly)	*Syrphus rectus*	1	0
Syrphidae (hoverfly)	*Syrphus ribesii*	41	16
Syrphidae (hoverfly)	*Syrphus torvus*	1	0
Syrphidae (hoverfly)	*Syrphus vitripennis*	5	0
Syrphidae (hoverfly)	*Syrphus vitripennis/rectus*	0	22

Table 3.S7 List of all insect flower-visitor species recorded in the warming experiment. Includes species type and recorded frequency for each species in each year.

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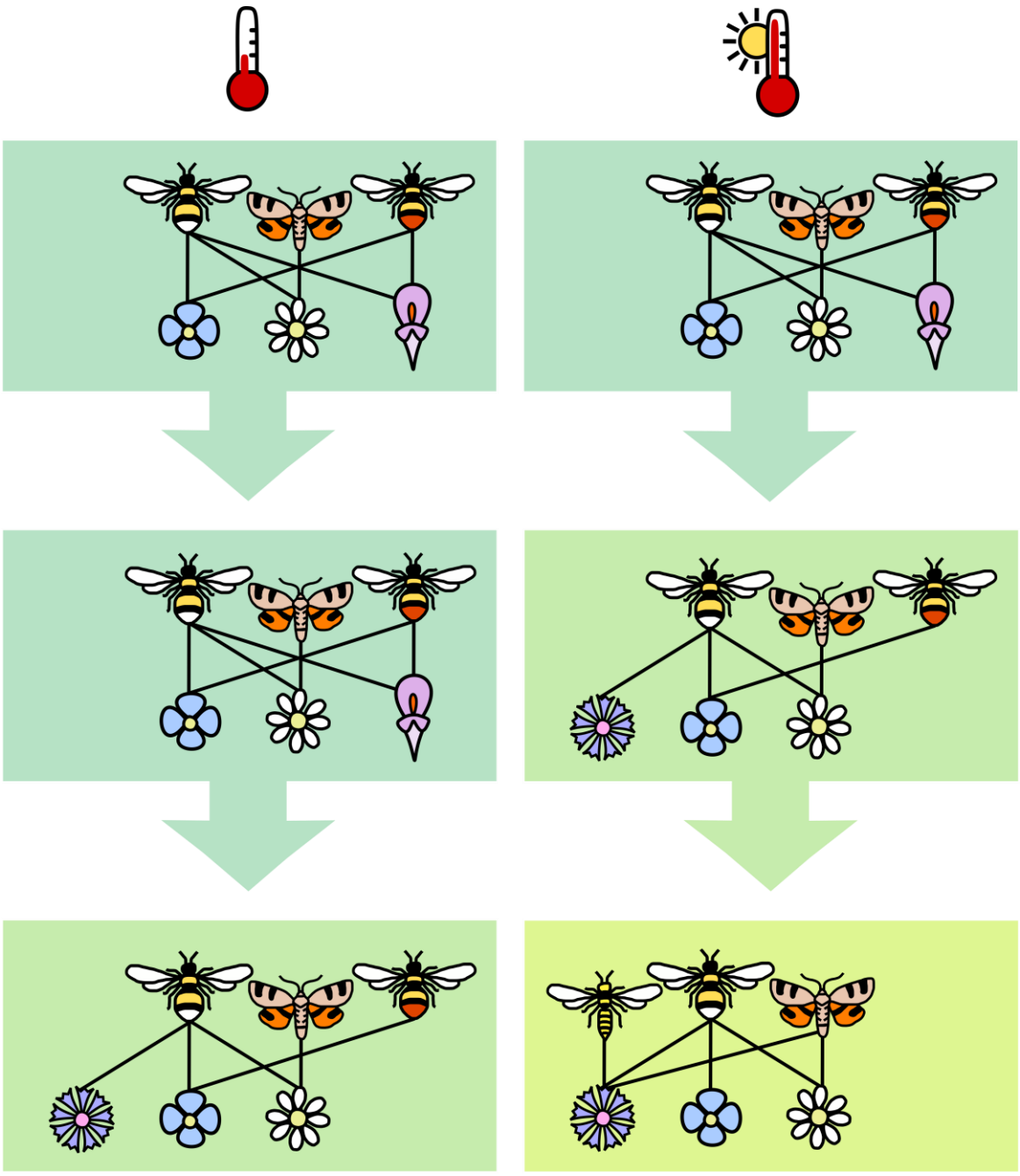
Chapter 4. Unravelling the temporal effects of simulated warming on plant-pollinator interactions within and between years



Abstract

The spatial and temporal impacts of climate change have been well documented across a broad range of organisms that includes pollinating insects and wildflowers; species are responding by moving to higher latitudes and/or altitudes and are displaying advanced phenology. However, very little is known about what climate change impacts there may be on whole communities of wildflowers and pollinators and the interactions between them. Both wildflower and pollinator communities display strong seasonality patterns via the natural turnover of species and their interactions as the seasons progress, but these temporal dynamics are largely overlooked in species interaction research and so far, no published studies have examined them in the context of climate change. In the majority of published network studies, the networks are created using data from a single sampling event or pooled across multiple sampling events, but this could obscure important temporal variation. Using an open-air field experiment employing infra-red heaters and additional rainwater in arable farmland, which was fully-replicated both spatially and temporally, we used ecological networks to investigate how increasing temperature and precipitation affected interactions between arable wildflowers and insect pollinators. We previously analysed our dataset in a temporally aggregated form, whereas in this chapter, we analyse the expanded dataset in order to investigate the week-to-week temporal dynamics, and responses to the simulated warming, of key aspects of the system: (1) wildflowers, (2) flower-visitors, (3) interaction frequency, and (4) interaction turnover. Simulated warming caused phenological advancement and reduced floral abundance for some species of wildflower, although the latter effect varied between years due to a significantly different flower community. Insect community composition varied greatly throughout the two seasons and between years, but it was similar between treatments apart from late summer in 2014 when warming strongly reduced the proportion of hoverflies. Interaction frequency varied throughout, and between, the two seasons; the treatment effects were also variable and appear to be mediated by insect community composition and ambient weather. Interaction turnover showed a gentle decline throughout the season in both years and was broadly similar between treatments, but the drivers responsible for it varied considerably between the two years and the treatments. Our findings suggest that future plant-pollinator research needs to account for, rather than ignore, potential within- and between-year temporal variation in both network structure, and interaction turnover.

4.1 Introduction

Pollinating insects play important roles in delivering several ecosystem services including the pollination of crops and wild plants, and opportunities for education and interactions with nature (IPBES, 2017). There are multiple pressures acting on pollinators that have directly reduced their abundances and distributions, these come from two main sources: agricultural management, which involves use of pesticides, increasing farmed land area, reducing semi-natural habitat, and changing crop rotations (Holzschuh et al., 2016; IPBES, 2017; Senapathi et al., 2017; Woodcock et al., 2016); and climatological changes, which includes earlier springs, more frequent floods and heatwaves, higher temperatures, and changes in precipitation (IPBES, 2017; Kerr et al., 2015; Parmesan, 2006). In addition, climate change has also been shown to cause phenological advancements in both plant and pollinator species (Hassall et al., 2017; Hegland et al., 2009; Kudo and Ida, 2013), which is a particularly important issue for plant-pollinator communities due to the seasonal nature of their life histories. The different timings of onset and cessation of flowering for all the plant species in a community combine with the different flight periods and feeding behaviours of all the insects to create a state of temporal dynamism, in which the community composition and the interactions between species change over time (CaraDonna et al., 2017; Olesen et al., 2008). Very few studies have investigated the temporal patterns in plant-pollinator communities, but those that have, demonstrated significant temporal interaction dynamics (Alarcón et al., 2008; Basilio et al., 2006; CaraDonna et al., 2017; Olesen et al., 2008; Petanidou et al., 2008). Climate change can directly upset these temporal dynamics by causing phenologies between interacting species to become mismatched if they don't advance at the same rate, which could cause species extinctions and have negative consequences on pollination services (Burkle et al., 2013; Kudo and Ida, 2013; Memmott et al., 2007). However, there is very little empirical evidence showing how climate change may impact whole communities of interacting organisms and currently there are no published studies demonstrating how it may affect temporal community dynamics. With current climate projections indicating temperature is likely to increase by 1.5^{o}C (relative to 1850-1900) by the end of this century (IPCC, 2013), it is critical that we understand the potential impacts this could have on communities of wildflowers and pollinating insects, and the ecosystem services they provide.

The temporal dynamics of both pollinator and plant communities, and the interactions between them, are poorly understood due to this topic being largely overlooked by the research community (CaraDonna et al., 2017). The vast majority of studies where interactions have been examined have done so with data that have been pooled across time; this is usually necessary to overcome issues of sampling completeness and small sample sizes that arise from the resource and time intensive sampling methods required to collect interaction data (Hegland et al., 2009). However, aggregating data can obscure the temporal dynamics of the system by masking any changes in community composition or behaviour, by averaging away strong but time-specific effects, and by incorporating "forbidden links" between species that do not temporally coexist (Basilio et al., 2006; CaraDonna et al., 2017). Pooling data is also particularly problematic in the case of climate change experiments as it could obscure evidence of phenological advancement. But, even if researchers do not pool their data, there is another methodological quandary that awaits them. Standard analysis of species interactions relies on constructing an interaction network that is then interrogated using network descriptors. Most of the commonly used descriptors, such as generality and vulnerability (see 1.3 in Chapter 1), examine the structural properties of a network. However, it is entirely possible that two networks created from the same site at two different time periods could display the same general structure, while the interactions within them are different (interaction turnover); this could be due to species turnover, and/or species interacting with different partners (interaction rewiring). These dynamics in community composition and behaviour are easily missed using structural network descriptors and therefore, additional analysis techniques that consider interaction turnover are required (Burkle and Alarcón, 2011; CaraDonna et al., 2017). This can be done using dissimilarity indices to compare the species and interaction composition of temporally adjacent interaction networks, which produces a series of comparisons showing the transition through time. Currently there are only a handful of published examples of this methodology for plant-pollinator networks, but each has used different indices: Jaccard in combination with a variation of the Simpson (Petanidou et al., 2008), Bray-Curtis (Burkle and Alarcón, 2011), and most recently Whittaker (via the Betalink R package (Poisot et al., 2012)) (CaraDonna et al., 2017). Another recent example from a plant-herbivore system used a variation of the Jaccard index (β_{cc}) (Kemp et al., 2017). It is unlikely that a standard methodology for this approach will emerge until consideration of temporal community dynamics becomes more widespread in community ecology.

In spite of the small number of published studies considering temporal plant-pollinator interaction dynamics, and the absence of a consistent analysis methodology, some interesting findings and general patterns have emerged. Baldock et al. (2011) examined variation in plant-pollinator networks at a very fine temporal scale, using 3-hourly periods to assess intra-daily differences in a Kenyan savanna habitat; they found evidence for significant differences in network structure between the 3-hourly time periods, but they didn't assess interaction turnover. Olesen et al. (2008) examined the day-to-day variation in an arctic plant-pollination network over two field seasons; they found network complexity and species richness increased steadily over time until a sudden collapse at the end of the season, determining these dynamics were driven by species' short flight-periods and flowering-times (species turnover), though they did not consider interaction rewiring. CaraDonna et al. (2017) investigated the week-to-week variation in interaction turnover in three years in a subalpine system; they found interaction turnover declined throughout each season but was generally high, and was primarily driven by interaction rewiring (changes in foraging behaviour) rather than species turnover. In one of the earlier temporal dynamics studies, Basilio et al. (2006) examined month-to-month variation in South American 'talar' forest plant-pollinator networks in a single calendar year; they found network size and connectance varied between months, but they did not consider interaction turnover. The coarsest temporal scale that can be found in the plant-pollinator literature is also by far the most common; many studies have collected data in multiple years and subsequently compared them to each other. Analysis of year-to-year variation in plant-pollinator networks provides some consistent results: while the structure of the networks and the numbers of species within them remain similar between years, the compositions of the species and interactions within them change significantly (Alarcón et al., 2008; CaraDonna et al., 2017; Dupont et al., 2009; Olesen et al., 2008; Petanidou et al., 2008). The reasons for this high interaction turnover are less consistent, with at least one study finding it is driven predominantly by species turnover (Petanidou et al., 2008), and another finding rewiring was more important (CaraDonna et al., 2017). All of these studies that investigated temporal dynamism in plant-pollinator communities agree that it is a crucial feature of these systems that should not be overlooked, and while many of them compared variation between years, none of them used the same temporal resolution to compare variation within years. The most appropriate intra-annual resolution to use in a given study will in-part be determined by practical aspects relating to field work, data analysis, and study system, but another

important element is the research question(s). Some subjects will be better suited to certain temporal scales; for example, investigations into phenological advancement as a result of climate change would be better suited to shorter time-scales (Burkle and Alarcón, 2011).

At present, there are no published examples of investigations into how the intra-annual temporal dynamics in plant-pollinator communities could be affected by climate change or any other environmental changes. However, there are a few studies that have looked at climate change impacts on plant-pollinator interactions that included assessment of phenological advancement and temporal mismatching. Using simulations, Memmot et al. (2007) looked at how phenologies could become mismatched under increased atmospheric CO_2 concentrations in a plant-pollinator interaction network; they found that phenological shifts caused reductions in food for pollinators during crucial periods, which could lead to extinctions of both plants and pollinators. Burkle et al. (2013) examined long-term observational datasets of plant-pollinator interactions and found evidence of temporal mismatches, changes in network structure, and species extinctions, though it is not clear how much this can be attributed to climate change as the study site also experienced land use change. Rafferty and Ives (2011) experimentally advanced the floral phenology of a selection of native plant species before observing pollinator visitation in the field, in Wisconsin (USA); they found that experimental advancement caused most of those plants that had shown historical advancement to receive more visits, and most of those that had not advanced historically to receive fewer visits. This experimental manipulation demonstrates that in some systems, and for some species, phenological advancement may not cause temporal mismatches. These studies have provided some valuable insights into how climate change may affect plant-pollinator interactions, but the only temporal aspect they can elucidate on is that of potential asynchrony.

In this study, we used a fully replicated experimental design to collect plant-pollinator interaction data on an arable farm in the north of England throughout two growing seasons, and in four separate climate change treatments. Interactions were sampled at approximately weekly intervals throughout the summer in two consecutive years to provide two series of week-to-week temporal time-slices, this resolution should be appropriate for investigating interaction turnover and other temporal dynamics with respect to climate change (Burkle and Alarcón, 2011; CaraDonna et al., 2017). Temperature was increased by 1.5 °C, which is aligned with current climate projections for Northern Europe

and weather models for the UK (IPCC, 2013; Kendon et al., 2014). Rainwater/precipitation was increased by 40%, which can either be interpreted as representing weather conditions in a wet summer, or a farmer increasing irrigation to mitigate the effects of a warmer and drier summer. The experimental method employed uses a bottom-up approach, whereby only the lowest trophic level is manipulated directly, but resultant changes in flower-visiting insects and species interactions can be observed in addition to the responses of the plants (Scherber et al., 2010). Due to the current absence of any previous studies investigating temporal plant-pollinator dynamics in the context of climate change, this study is necessarily exploratory in nature and is intended to be hypothesis-forming rather than led. I wished to answer four main questions: (1) What are the seasonal and annual patterns in plant flowering and are they affected by the climate change treatments? We know from analysis of the aggregated dataset in Chapter 3 that the simulated warming reduced overall floral abundance in both years, and that it was higher in the second year, so we could expect to see some difference between the two years in the temporal pattern or its magnitude. We also know that UK plants are advancing phenology in response to climate change (Dunne et al., 2003; Fitter and Fitter, 2002; Sparks et al., 2000). It is logical that floral abundance may fluctuate throughout the seasons as the community changes, and possible that different plants within the community may have differing sensitivities to the treatments; (2) How does the composition of the insect community change throughout, and between, the two seasons and does it respond to the treatments? Given that the collapsed dataset showed a clear difference in insect community between the two years (see Figure 3.5 in Chapter 3), and that several interaction studies have found significant differences in community composition between years (Alarcón et al., 2008; Olesen et al., 2008; Petanidou et al., 2008), we expected that the observed difference in composition between the two years would prove to be significant when analysed. Our previous analysis of this dataset also showed that treatment only had a significant effect on insect visitation in one of the years (see Figure 3.3 in Chapter 3), which suggests that some species groups may be more strongly affected by the simulated warming than others; (3) What are the seasonal and annual patterns in interaction frequency and are they affected by the climate change treatments? Because the aggregated data analysis showed a significant effect of treatment on insect visitation in only one of the years, it seems likely that the temporal patterns for these two years are different from one another and that there would be an effect of treatment on interaction frequency over time but not necessarily in both years; (4) How does interaction turnover change throughout, and

between, the two seasons and what is driving it? How do these dynamics respond to the climate change treatments? We know from previous studies using day-to-day (Olesen et al., 2008) and week-to-week (CaraDonna et al., 2017) temporal resolutions that interaction turnover can be highly variable throughout a season. We also know that the driver of this interaction turnover can be species turnover (Olesen et al., 2008) and/or interaction rewiring (CaraDonna et al., 2017). It seems likely that our dataset would show similar fluctuations in interaction turnover, but we can only speculate as to if and how this may be affected by the treatments.

4.2 Methods

4.2.1 Experimental design and data collection

All of the data used in this Chapter were collected from the same experiment as that in Chapter 3. For full details of the experimental design please see section 3.2.1 in Chapter 3 and Berthe et al (2015). For full details of the data collection please see 3.2.2 in Chapter 3.

The experiment was conducted on a conventionally managed arable farm in North Yorkshire (Stockbridge Technology Centre, 53°49'N–1°9'W), in a field sown with spring wheat (*Triticum aestivum* cultivar Tybalt) and several species of arable wildflowers (see Table 3.S1 in appendix 3.6.1 in Chapter 3 for species list and sowing weights, and 3.2.1 for selection criteria). The experimental setup and manipulations replicated those of Rollinson and Kaye (2012); we established a replicated, randomized block open-field experiment consisting of six replicates of four simulated climate-change treatments: 1.5 °C increase in temperature above ambient ('HEAT'); 40% increase in precipitation ('WATER'); warming and precipitation treatments combined ('HEAT+WATER'); and ambient conditions ('CONTROL'). Experimental plots were 2×2m and separated by a 2m buffer of wheat (see Figure 3.S1 in Chapter 3 for experimental layout), those plots in the warmed treatments had infra-red heaters suspended 1.5m above them, while the remaining plots had non-functional 'dummy' heaters to mimic any shading effects. The temperature elevation was constant and maintained at the correct level via feedback from digital sensors in both heated and unheated plots. Increased rainfall was simulated in the watered plots via hand watering, volumes were based on mean monthly rainfall data collected between 2002 and 2011 at the

farm's weather station. The experiment was run over two growing seasons: 16/04/14 - 19/08/14, 15/04/15 - 18/08/2015.

Plot observations were carried out to collect information on species interactions. Each of the 24 2x2m experimental plots was observed for a total of 20 minutes per sampling round; 7 rounds were completed between early June and late August in 2014 and 2015, allowing for approximately one-week intervals between rounds (weather permitting). Sampling dates were matched as closely as possible to ensure even sampling between years. Insect specimen were caught using a hand-net while feeding from flowers and identified later using morphological keys. Sampling occurred on all wildflowers present in each plot, including non-sown species. Before the start of every timed plot observation, all flowering plant species were recorded and floral units were counted (Forup et al., 2008). Percentage cover estimates for all plant species in each plot were recorded several times during each field season.

4.2.2 Data analysis: Wildflowers

Flowering plant species richness and floral abundance were analysed using generalised linear mixed effects models (GLMMs) with the 'lme4' package (Bates et al., 2015) in R version 3.2.3 (R Core Team, 2015). The models included treatment and sample round as fixed effects with an interaction term and plot as a random effect; significance of the fixed effects and interaction was determined via likelihood ratio tests. The interaction term was non-significant for floral richness in either year and so the models were re-run without it. Floral richness was analysed using poisson error distribution, while total floral abundance was analysed using negative binomial error due to overdispersion. Community dissimilarities for flowering plants between the two years were assessed via the Bray-Curtis method using the adonis function of the 'vegan' package (Oksanen et al., 2016) for R.

4.2.3 Data analysis: Flower-visitors

Species accumulation curves were created for each sample round to examine sampling completeness of insect visitors. Asymptotes were not reached, so species richness was extrapolated, and Chao estimates (Chao, 1987) of richness calculated using the package vegan in R. However, due to the strong potential for advanced phenology in the heated plots

it appeared to be more appropriate to separate the treatments and create Chao estimates for each round in each treatment. Unfortunately, these sample sizes were very variable, which resulted in very large error estimates and some unrealistic richness estimates; the same is true for values when data from the treatments are combined (see Table 4.S2 in appendix 4.6.2). As a result of this unreliability, and given the replicated and standardised nature of the methodology, raw species richness values were examined instead. Visitor richness was analysed using GLMMs with poisson error distribution, plot as a random effect, a treatment:round interaction as a fixed effect, and mean air temperature (daily means from only those dates when sampling occurred, as recorded by the farm's weather station) as a fixed effect. Using likelihood ratio tests, the interaction term was found not to be significant for 2015 and air temperature was not for 2014, so these elements were dropped from the models. Community dissimilarities for flower visitors between the two years were assessed via the Bray-Curtis method using the adonis function of the 'vegan' package (Oksanen et al., 2016) for R.

4.2.4 Data analysis: Interaction frequency

Sampling completeness of interactions was also examined, using the same method as for visitor richness, but once again estimated values were unreliable (see Table 4.S3) and so the raw values were analysed. The total number of interactions (flower visits) per round and number of unique interactions (pairings between specific flower and insect-visitor species) per round were analysed using GLMMs with poisson distribution, except for the total interactions in 2015, which used negative binomial after poisson failed to converge. Significance of the fixed effects and interaction was determined via likelihood ratio tests. The models included plot as a random effect, a treatment:round interaction term as a fixed effect, and mean air temperature (daily means from only those dates when sampling occurred) as a fixed effect, except for unique interactions in 2014 where temperature was not significant and was dropped from the model.

4.2.5 Data analysis: Interaction turnover

To further investigate the temporal dynamics of the species interactions, we examined the turnover of interactions between successive sampling rounds via the 'betalink'

package (Poisot et al., 2012) for R. This package calculates four different components of network dissimilarity using one of the twenty-four common, presence-based beta diversity measures compared in Koleff et al. (2003). These components are: dissimilarity in species composition (β_S), interaction turnover (β_{WN}), contribution of interaction rewiring to interaction turnover (β_{OS}), and contribution of species turnover to interaction turnover (β_{ST}), where interaction turnover = interaction rewiring + species turnover ($\beta_{WN} = \beta_{OS} + \beta_{ST}$). These measures were calculated for each successive sampling round comparison (e.g. rounds 1 and 2, then 2 and 3 etc.), for each treatment, in each year. Unfortunately, the networks for individual plots in each sample round were too small for analysis, so the data were necessarily pooled across the plots in each treatment. Following the conclusions of Koleff et al. (2003), both a broad-sense (β_{cc}: the complementary beta diversity measure to the Jacccard index) and a narrow-sense (β_{sim}: Lennon index) beta diversity measure were employed; broad-sense measures focus on the level of species/interaction overlap between two samples, while narrow-sense measures also focus on the proportions of gains and losses from one sample to the next, which means they can account for differences in species/interaction overlap that are due to unequal numbers of species/interactions. β_{cc} and β_{sim} are commonly used diversity measures (Kemp et al., 2017; Novotny, 2009; Senapathi et al., 2015) expressed as a value between 0 and 1, where a low value represents low dissimilarity or turnover, for example: $\beta_{WN} = 0$ would be returned where there has been no change in interactions between two successive sampling rounds.

4.3 Results

4.3.1 Wildflowers

Flowering plant community composition was significantly different between the two years ($F(1)=19.63$, $p=0.001$) and flowering plant species richness was far lower in all but the first sample round in 2015 when compared to 2014 (Table 4.1). The percentage cover of the crop plant wheat (*T. aestivum*) was lower in 2015 compared to 2014, while that of the most abundant sown wildflower was much higher in 2015 (Figure 4.1). Floral richness was not significantly affected by treatment in either year (Table 4.S4 in appendix 4.6.2) but was by sample round (2014 Round: $\chi^2(6)=24.771$, $p<0.001$; 2015 Round: $\chi^2(6)=36.14$, $p<0.001$). Floral abundance was significantly affected by treatment in both 2014 and 2015, but only during some of the sample rounds (Treatment:Round interaction, 2014: $\chi^2(18)=69.393$,

$p<0.001$; 2015: $\chi^2(18)= 103.54$, $p<0.001$). The general pattern in each year is that both heated treatments have lower floral abundance than the unheated; this is strongest in sample rounds 2, 5, 6 and 7 in 2014, and in rounds 1 and 2 in 2015 (Figure 4.2). There is a clear difference between the two years in terms of the temporal floral abundance pattern: in 2014 there are two obvious peaks, which represent spring flowering species (rounds 1-2) and summer flowering species (rounds 5-6), but in 2015 there is no second peak. The temporal abundance pattern for all species in 2014 is mirrored by those for the three most common sown wildflowers: *L. purpureum* (a spring species) corresponds with the first peak, while *G. segetum* and *C. cyanus* (summer species) match the second (Figure 4.2). However, the same is not true of 2015; where we see relatively low abundance and a plateau in rounds 5-7 for all species combined, there is a gradual increase and relatively high abundance values for the two summer species (*G. segetum* and *C. cyanus*).

There is some evidence of phenological advancement in the temporal floral abundance pattern: where there are steep declines that represent the loss of early species, they are advanced by one sample round for the heated treatments. There is further evidence for advanced phenology from the three most abundant of the sown wildflowers: *L. purpureum* ceased flowering one round sooner in HEAT and HEAT+WATER than CONTROL in both years, while *G. segetum* started flowering one round sooner (Figure 4.2).

	Plant species richness						
	Round	Round	Round	Round	Round	Round	Round
Year	1	2	3	4	5	6	7
2014	9	17	23	21	20	20	16
2015	9	11	13	8	13	12	12

Table 4.1 Total number of plant species found in each sampling round for 2014 and 2015

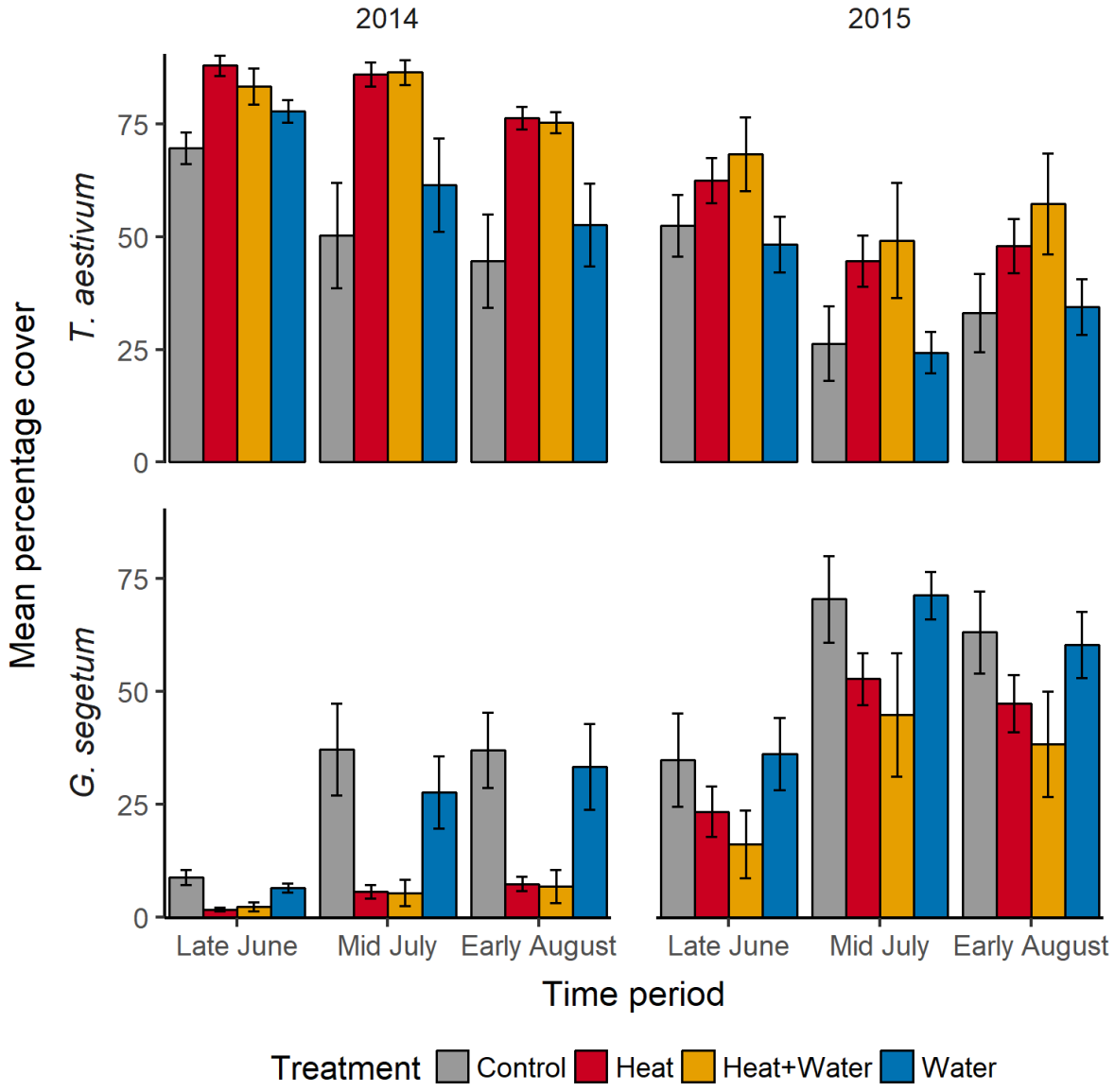


Figure 4.1 Comparison of mean percentage cover (with standard error bars) for the crop plant and the most abundant sown wildflower species at three different time points during the field season, in each treatment, and in both years. The time periods correspond to the following sample rounds: late June = round 2, mid-July = round 4/5, early August = round 6/7.

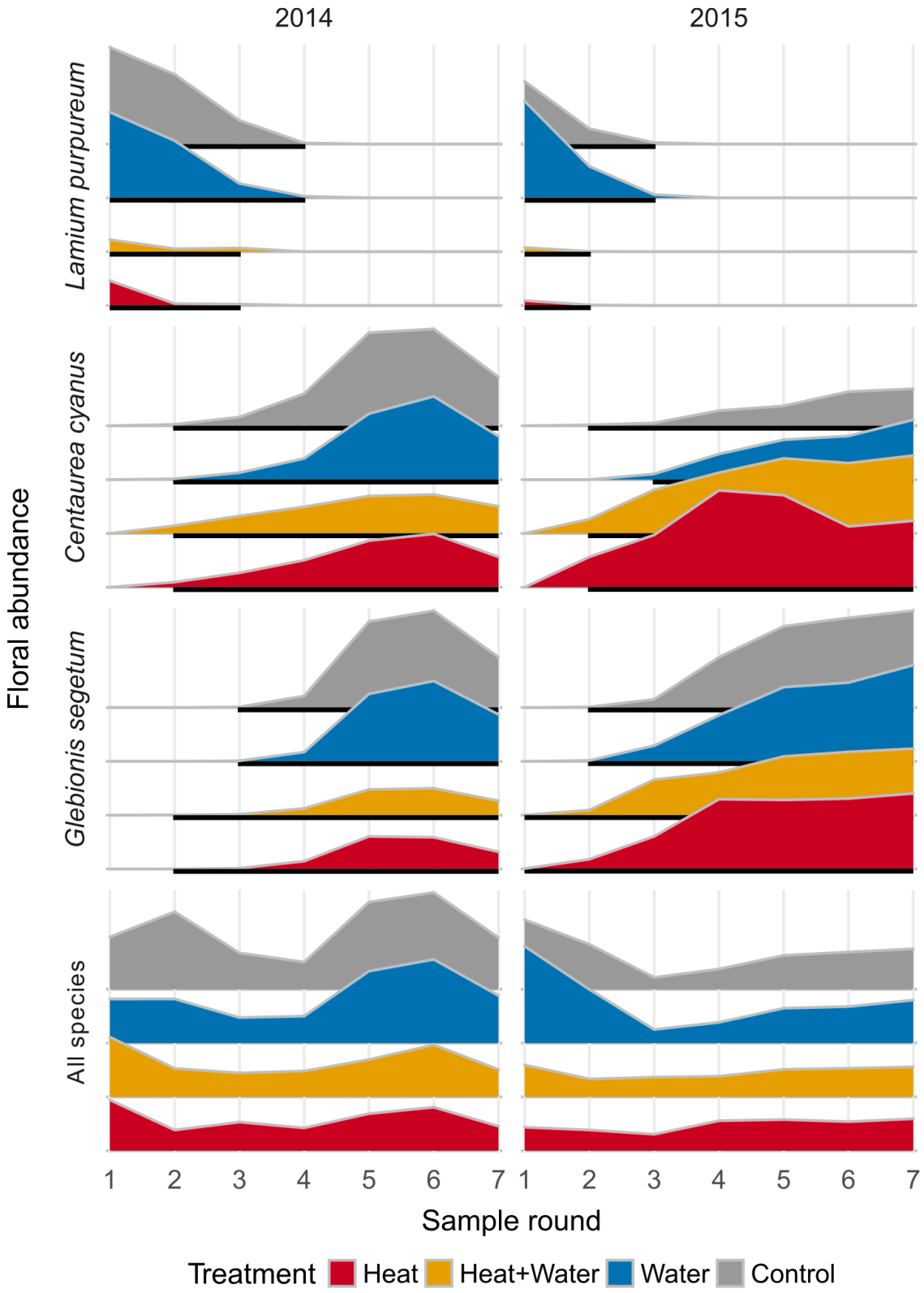


Figure 4.2 Comparison of floral abundance and phenology through time and across treatments for the three most abundant species of wildflower, and for all flower species combined. Abundance values are totals summed across all experimental plots in each treatment for each sample round. Black lines under the polygons represent the recorded flowering periods. The y-axes are scaled for each panel's maximum abundance range: 0-2462 for *L. purpureum*, 0-476 for *C. cyanus*, 0-1500 for *G. segetum*, and 0-3915 for all species combined.

4.3.2 Flower-visitors

The composition of the insect flower-visitor community was significantly different between 2014 and 2015 ($F(1)=32.63$, $p=0.001$). Hoverflies (syrphidae) dominated the community in the first year of the experiment, especially during round 5 when there was a spike in their numbers (Figure 4.3). The community in 2015 is initially dominated by wild bees and wasps (mainly bumblebees, *Bombus sp.*), but they start to decrease in abundance from round 5, while hoverflies and honeybees (*Apis mellifera)* gradually increase. There appears to be little impact of the simulated warming treatments on broader community composition, except for hoverflies in 2014, where there is a much smaller spike in numbers in rounds 5 and 6 for both HEAT and HEAT+WATER when compared to CONTROL. Raw visitor richness was significantly affected by treatment in 2014 but only during some of the sample rounds (Treatment:Round interaction: $\chi^2(18)=29.834$, $p=0.039$), while air temperature had no effect (Table 4.S5 in appendix 4.6.2). In 2015, treatment had no significant effect on visitor richness (Table 4.S5), but sample round and air temperature did (Round: $\chi^2(6)=244.578$, $p<0.001$; Temperature: $\chi^2(1)=4.353$, $p=0.037$).

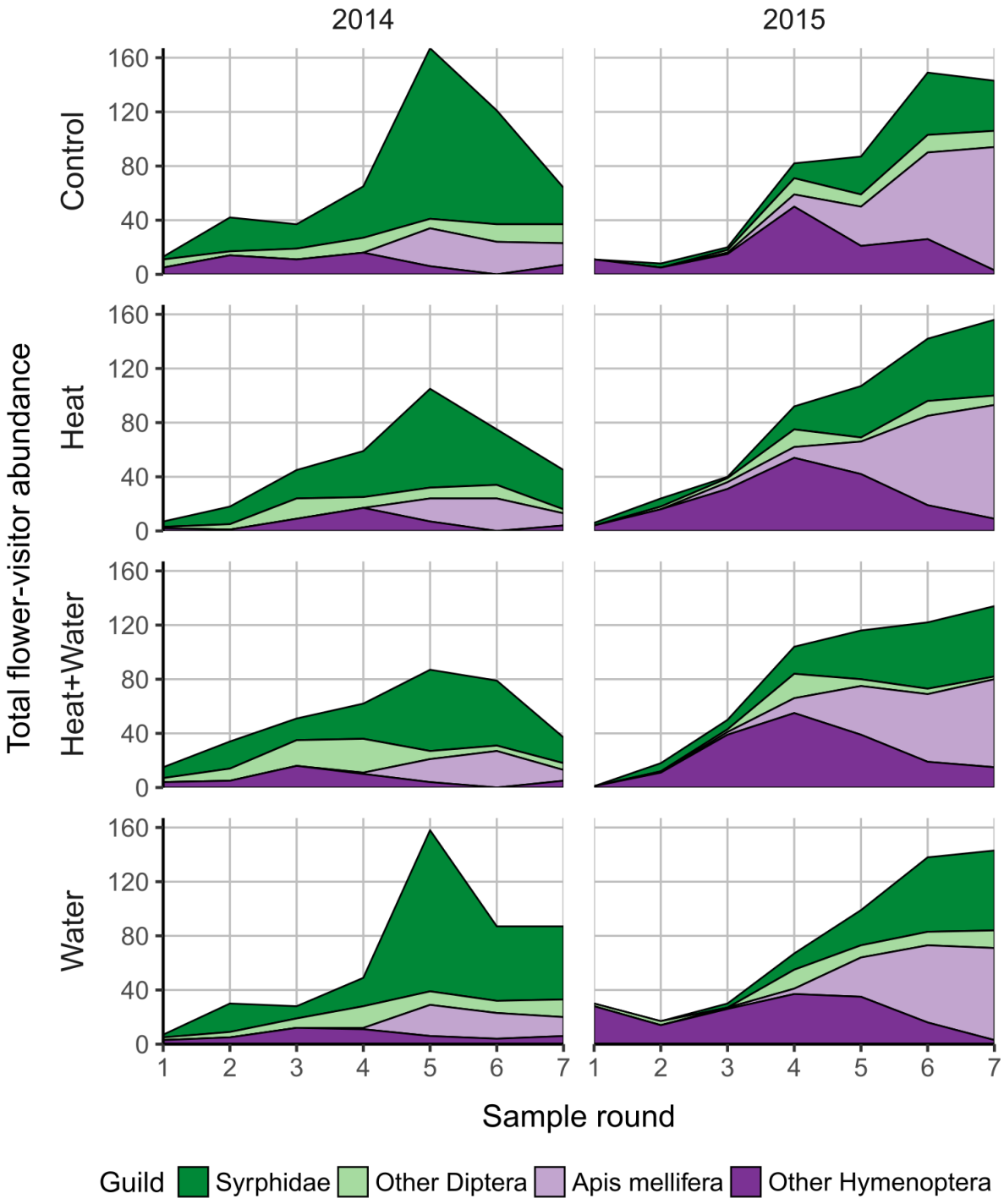


Figure 4.3 Comparison of total flower visitor abundance during each sample round, for each treatment and for each year. Abundance values are totals summed across all experimental plots in each treatment for each sample round. The proportions of the total abundance that represent the four main insect types are shown in different colours. About 95% of "Other Hymenoptera" abundance consists of visits by *Bombus* species (Bumblebees).

4.3.3 Interaction frequency

In both years, the total number of flower-visitor interactions was significantly affected by ambient air temperature and by treatment, though the latter effect was only present in some of the sample rounds (2014 Treatment:Round interaction: $\chi^2(18)=65.294$, $p<0.001$; 2014 Temperature: $\chi^2(1)=5.553$, $p=0.018$. 2015 Treatment:Round interaction: $\chi^2(18)=63.940$, $p<0.001$; 2015 Temperature: $\chi^2(1)=4.825$, $p=0.028$). The same was true of the number of unique interactions in 2015 (Treatment:Round interaction: $\chi^2(18)=38.541$, $p=0.003$, Temperature: $\chi^2(1)=5.462$, $p=0.019$), while in 2014 air temperature had no effect (Table 4.S6 in appendix 4.6.2), but the interaction between treatment and sample round was once again significant (Treatment:Round interaction: $\chi^2(18)=35.358$, $p=0.009$). There is no general pattern of treatment effects on interactions as there is a lot of variation both within and between years and interaction measure. In 2014 there are far lower values of both total and unique interactions in both of the heated treatments compared to the unheated ones in round 5, and to a lesser extent rounds 6 and 7 for total interactions and rounds 4 and 7 for unique (Figure 4.4). There is also a weak positive effect of simulated warming on both total and unique interactions in round 3 in 2014. There is a different picture for 2015; simulated warming caused a strong reduction in both total and unique interactions in sample round 1, and for unique interactions in rounds 4 and 6, but in rounds 2 and 3 we see the reverse effect of warming clearly increasing total and unique interactions (Figure 4.4). The temporal patterns for total and unique interactions in 2014 are very similar, but in 2015 the patterns diverge at round 4, thereafter the values continue to increase for total interactions while they remain relatively stable for unique.

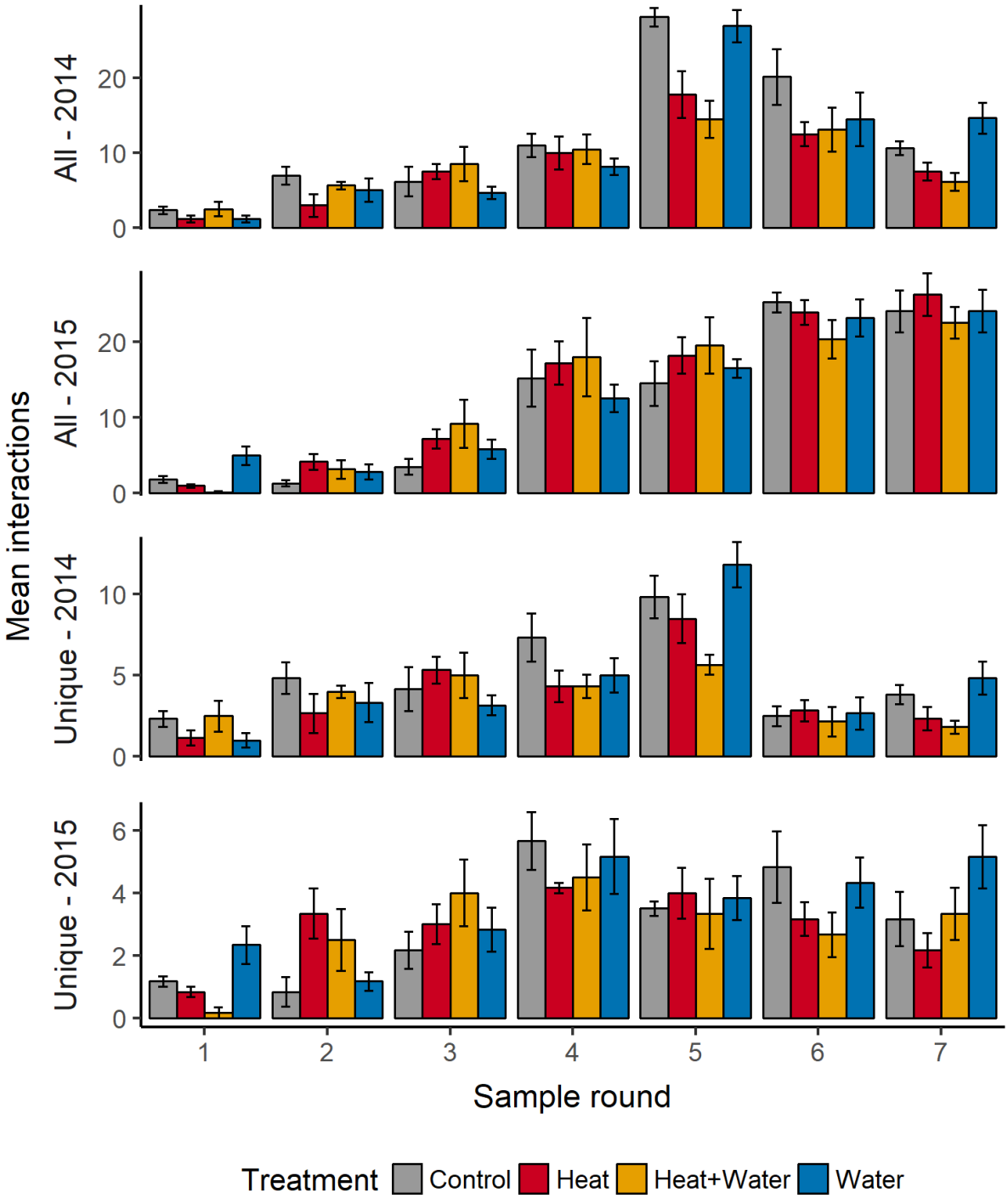


Figure 4.4 Comparison of both the mean number of interactions and the mean number of unique interactions, for each treatment (with standard error bars), in each sampling round and each year.

4.3.4 Interaction turnover

Examination of the outputs from the interaction turnover analysis using the betalink package revealed that the results were similar for both of the diversity measures we employed, but the β_{sim} (Lennon Index) displayed more extreme treatment effects. As a result of this and for the sake of brevity, only those using the β_{cc} (adjusted Jaccard Index) diversity measure will be shown and discussed in the main body of the text. The results for the β_{sim} (Lennon Index) diversity measure can be found in appendix 4.6.2 (Figure 4.S2). It should be noted that where there are very high values of β_S, the values of β_{ST} become unreliable and as a result some of the β_{ST} values from the Jaccard results should be viewed with caution: the first sample round transition for all treatments in 2014, and HEAT at transition 4 in 2014 (Figure 4.5). The results from the first transition in 2015 may be viewed with less caution, given that the effects are extremely consistent between both heated treatments and both unheated ones, and that the results from the previous analyses have already demonstrated that the additional watering has very little effect on any aspect of the flower or insect community (Figures 4.1, 4.2, 4.3 and 4.4).

The values for both β_S (species turnover) and β_{WN} (interaction turnover) start high in 2014, which indicates great changes in the community between the first two sample rounds; β_{WN} decreases gradually over the sample round transitions while β_S has a sharp decrease followed by more of a plateau (Figure 4.5). Despite high variation in β_{OS} (interaction rewiring) and β_{ST} (interaction turnover caused by species turnover) in 2014, it appears that β_{OS} generally decreased over the season while β_{ST} increased. In 2015 the values for β_S and β_{WN} are more variable, but once again show a gradual decline throughout the season from a high starting value. In contrast to the values from 2014, β_{ST} generally decreased over the season in 2015 while β_{OS} fluctuates without overall change. In 2014 both β_S and β_{WN} appear to be minimally affected by the climate warming treatments, though there is a spike in β_S values for the WATER treatment at transition 3 and one in the HEAT treatment at transition 4. The treatment effects are more marked for β_{OS} and β_{ST} in 2014, with each treatment displaying a very different pattern. The treatments appear to have had stronger effects on β_S and β_{WN} in 2015 than for 2014; the two heated treatments have a high turnover of species and interactions in the first transition, which then drops sharply in transition 2 and is followed by more a gentle decline, whereas the two unheated treatments show the opposite initial pattern of much lower values that are followed by an increase (Figure 4.5). The values

of β_{OS} and β_{ST} are much more uniform between the treatments in 2015 than for 2014; β_{OS} appears to be lower in both heated treatments than unheated while β_{ST} appears to be higher in the heated treatments but only at the very start and towards the end of the season.

Figures 4.6-4.9 show the species interaction networks for each sampling round for each treatment in 2014, Figures 4.10-4.13 display the same for 2015, and as such display the changes in community, interaction and network structure through time. Examination of these networks reveals some additional patterns. In 2014, starting from sample round 5, the community of visited plants decreases in size and becomes dominated by two species: G. segetum and C. cyanus; this effect is less noticeable in 2015 as the wildflower species richness is far lower than in 2014. Due to this lower plant diversity, the networks for sample rounds 1-3 in 2015 are far simpler than their 2014 counterparts. These network plots show phenological advancement of the early spring species of wildflower (those at the bottom of the y-axis in Figures 4.6-4.13) by approximately one sample round under simulated warming, and as a result the shift in network structure that accompanies the loss of these species is also advanced.

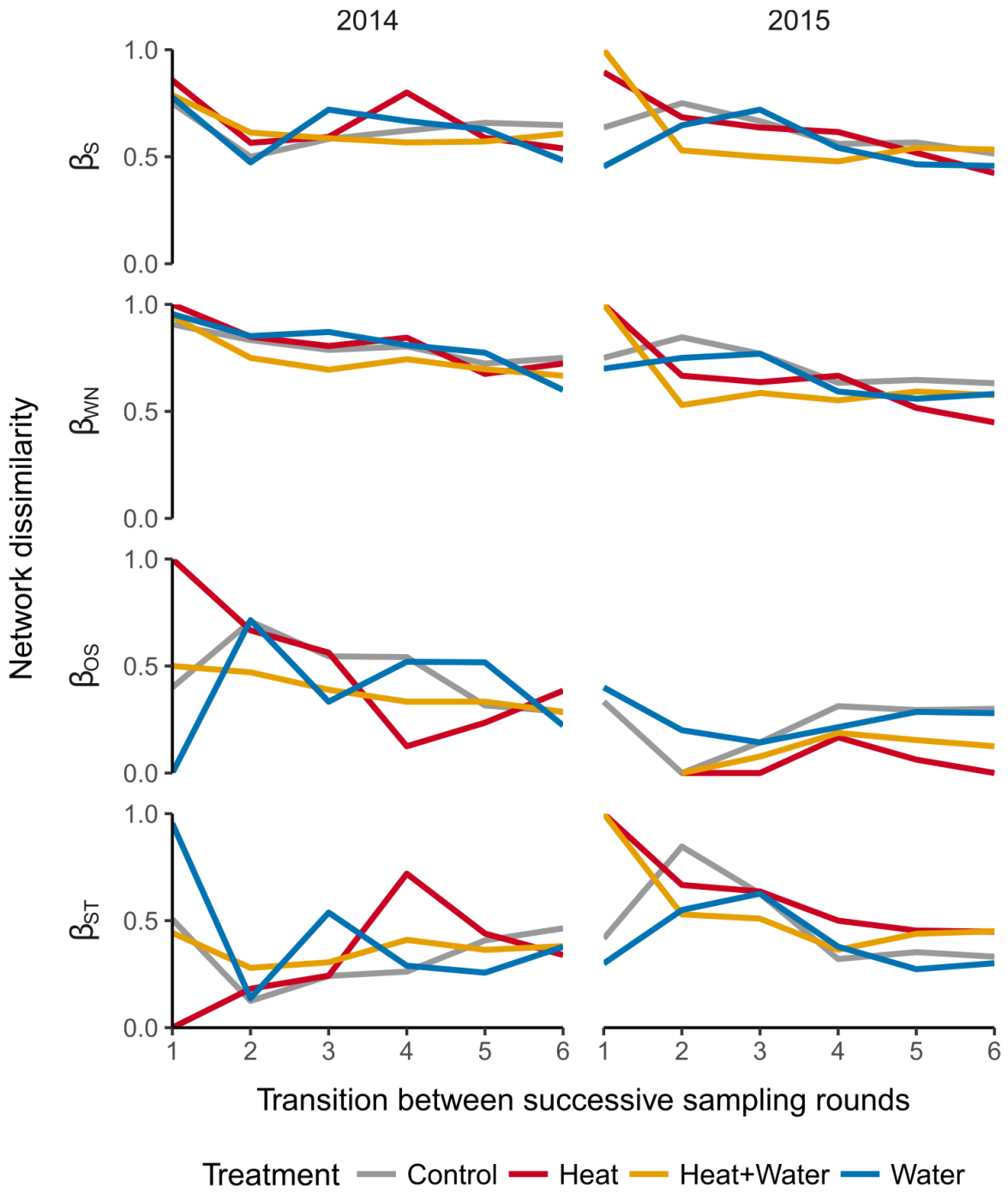


Figure 4.5 Comparison of the within-season and between-years temporal dynamics for each treatment. The x axis represents comparisons of temporally adjacent networks from successive sample rounds. The y axis represents the four different measures of network dissimilarity: β_S is species turnover from one round to the next, β_{WN} is interaction turnover, β_{OS} is the contribution of interaction rewiring to interaction turnover, and β_{ST} is the contribution of species turnover to interaction turnover.

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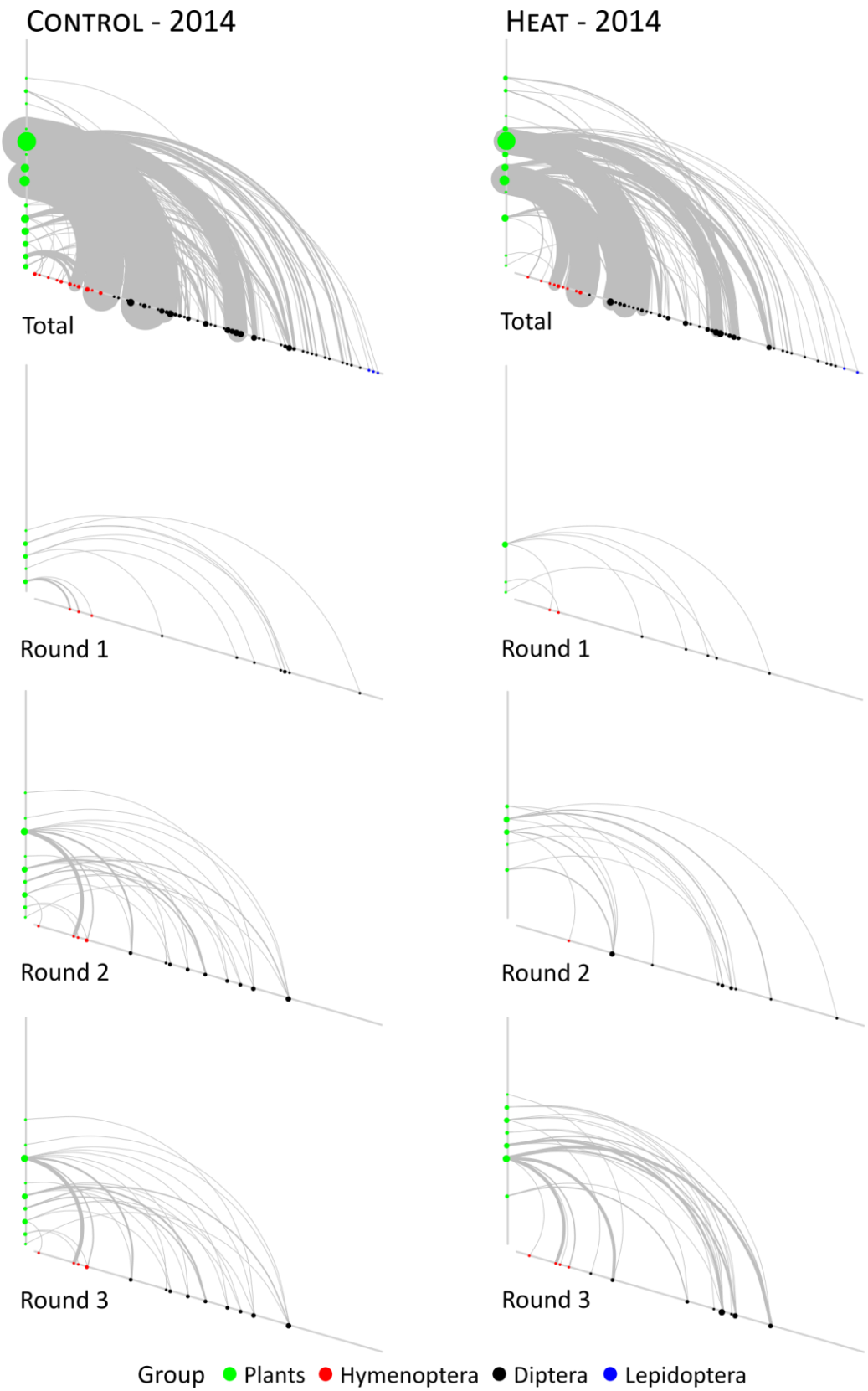

Figure 4.6 Comparison of the network structure and phenology for the combined total network and the individual temporal networks from sample rounds 1-3, from the CONTROL and HEAT treatments in 2014. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

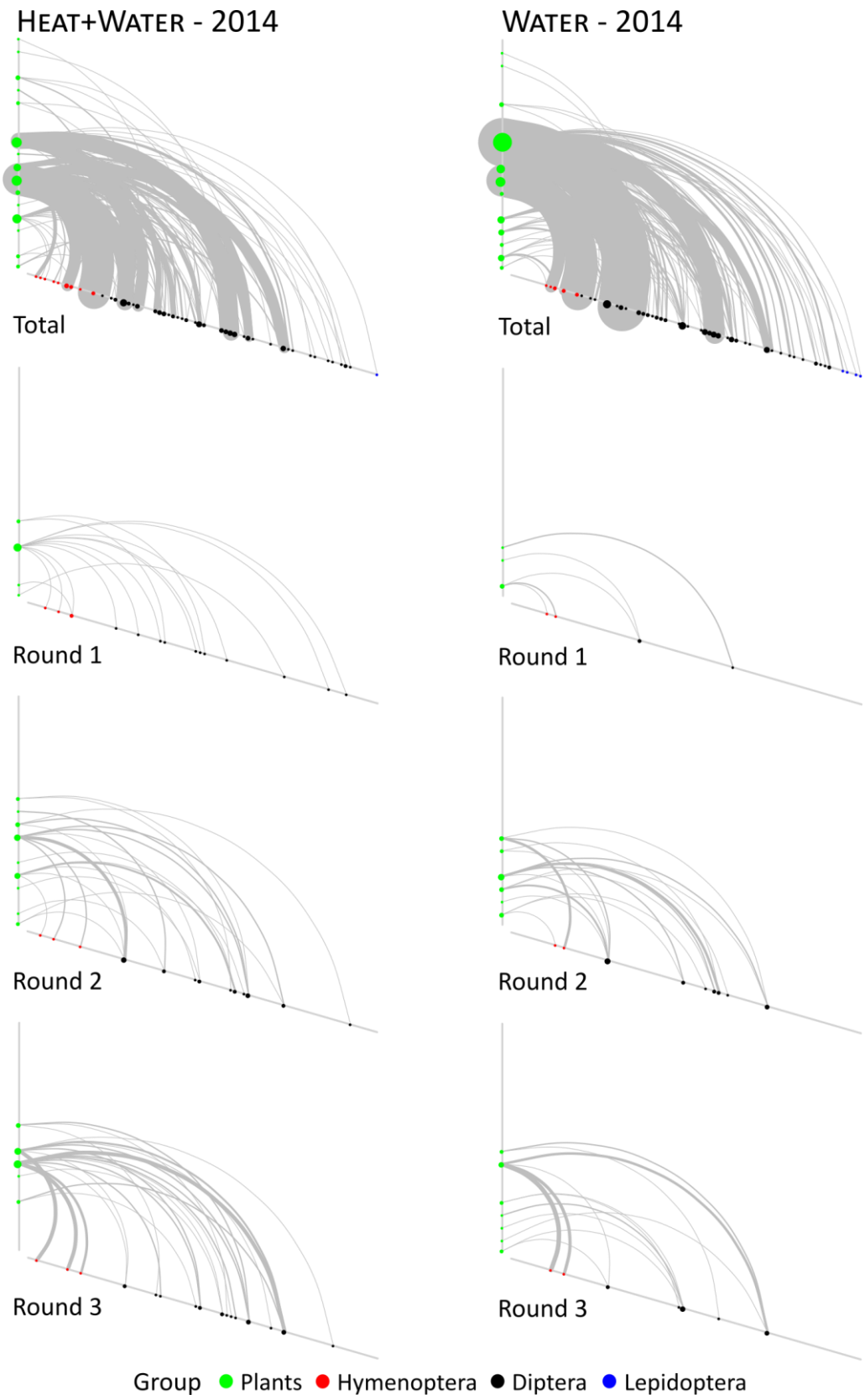

Figure 4.7 Comparison of the network structure and phenology for the combined total network and the individual temporal networks from sample rounds 1-3, from the HEAT+WATER and WATER treatments in 2014. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

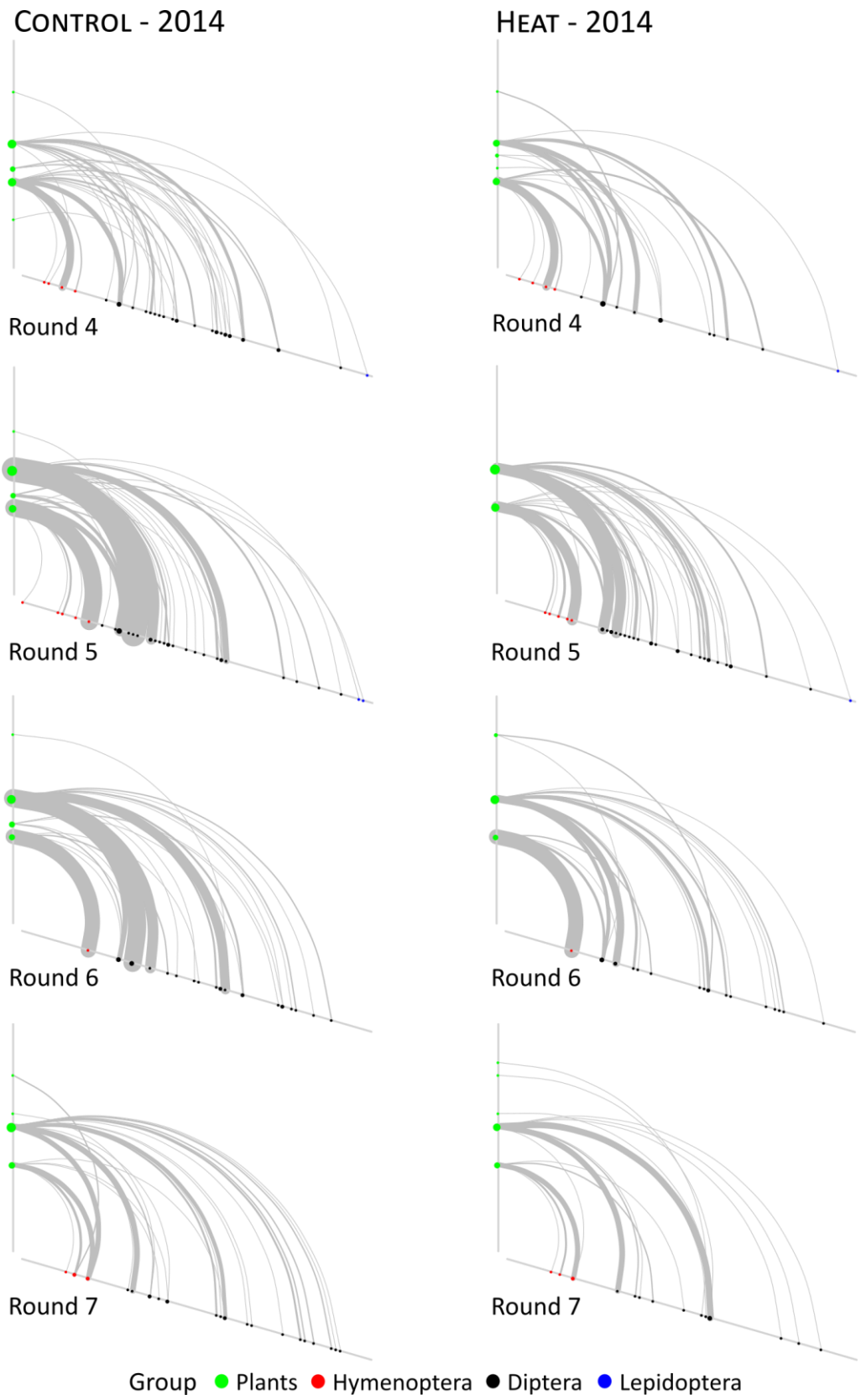

Figure 4.8 Comparison of the network structure and phenology for the individual temporal networks from sample rounds 4-7, from the CONTROL and HEAT treatments in 2014. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

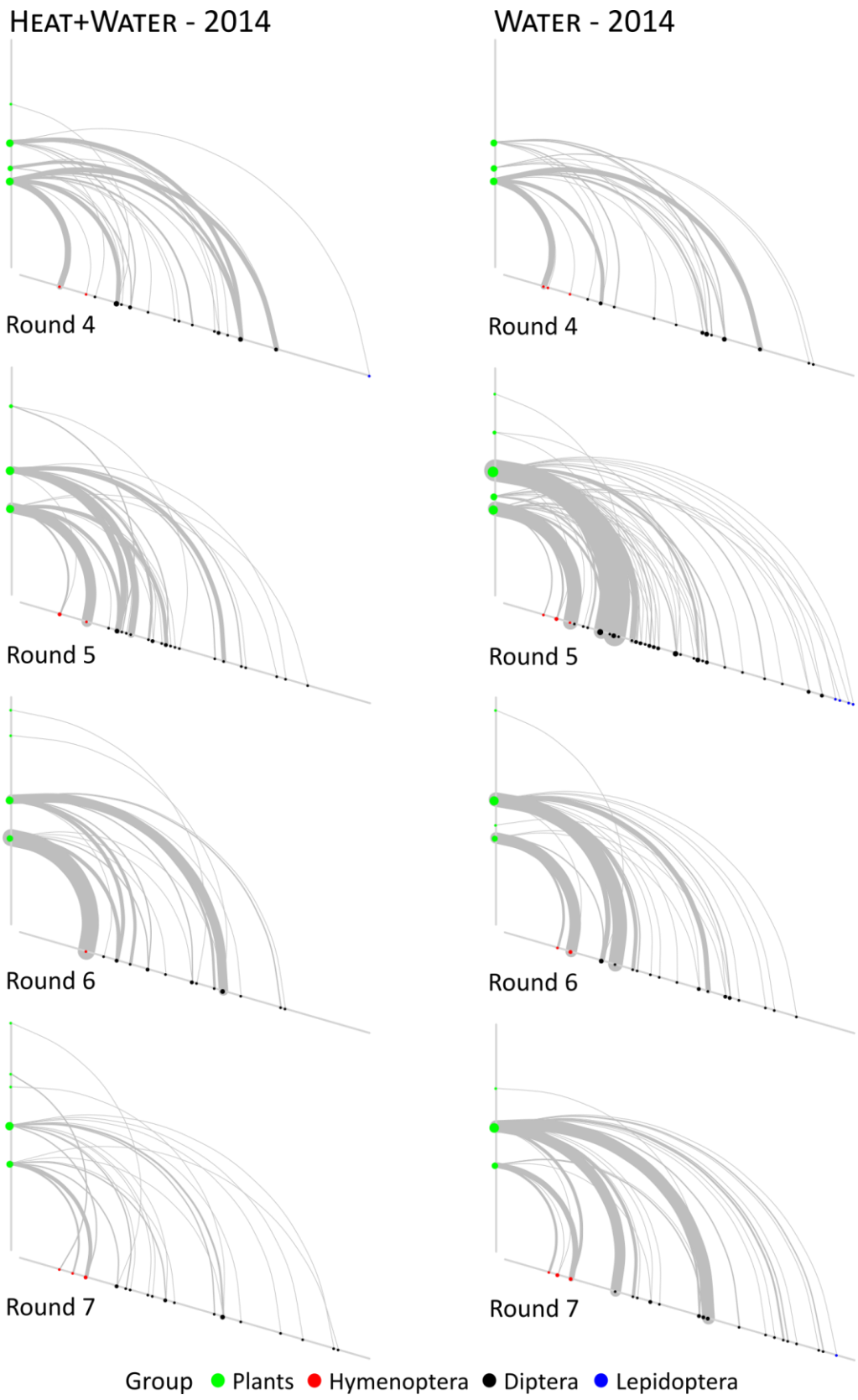

Figure 4.9 Comparison of the network structure and phenology for the individual temporal networks from sample rounds 4-7, from the HEAT+WATER and WATER treatments in 2014. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

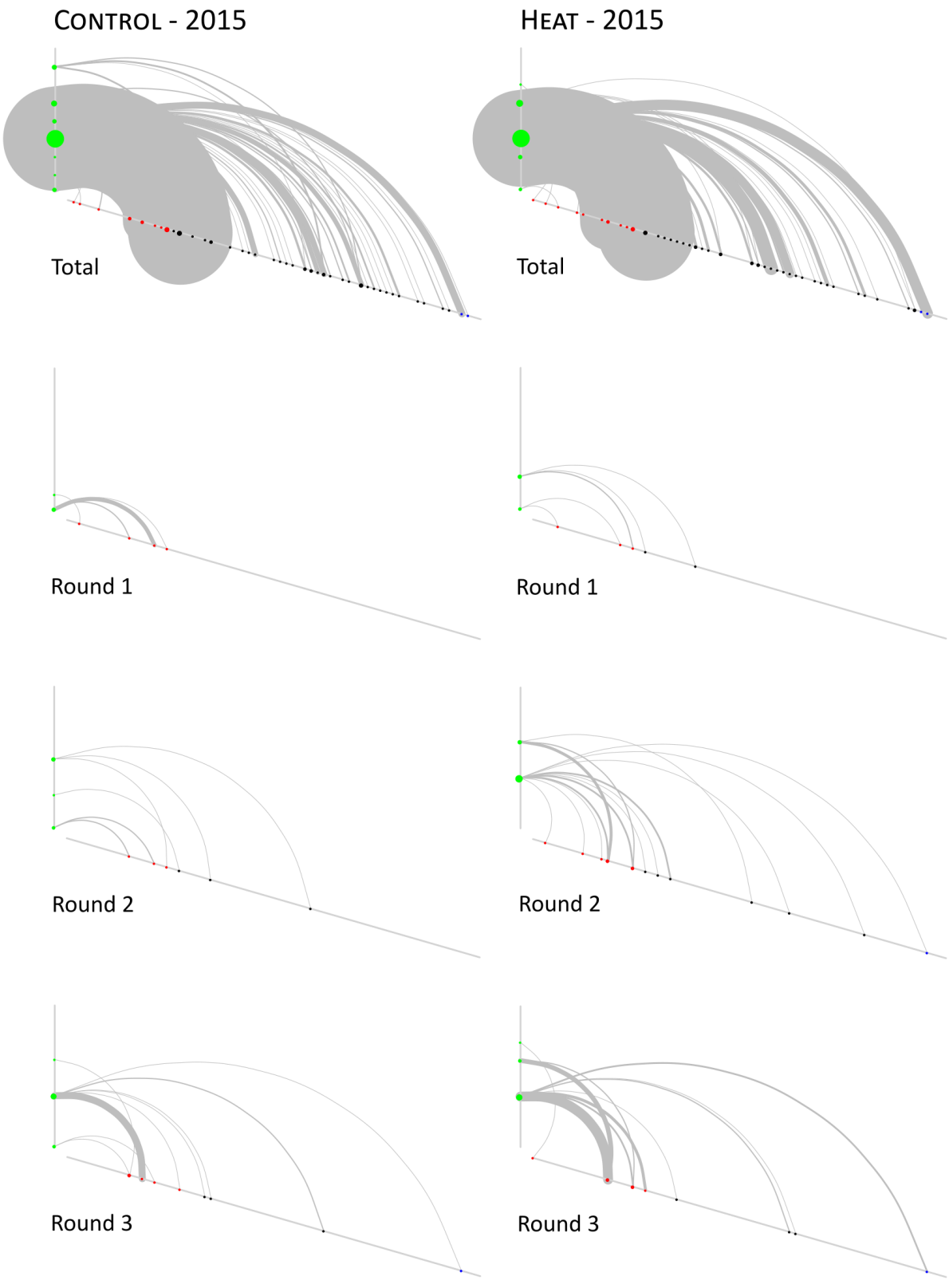

Figure 4.10 Comparison of the network structure and phenology for the combined total network and the individual temporal networks from sample rounds 1-3, from the CONTROL and HEAT treatments in 2015. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

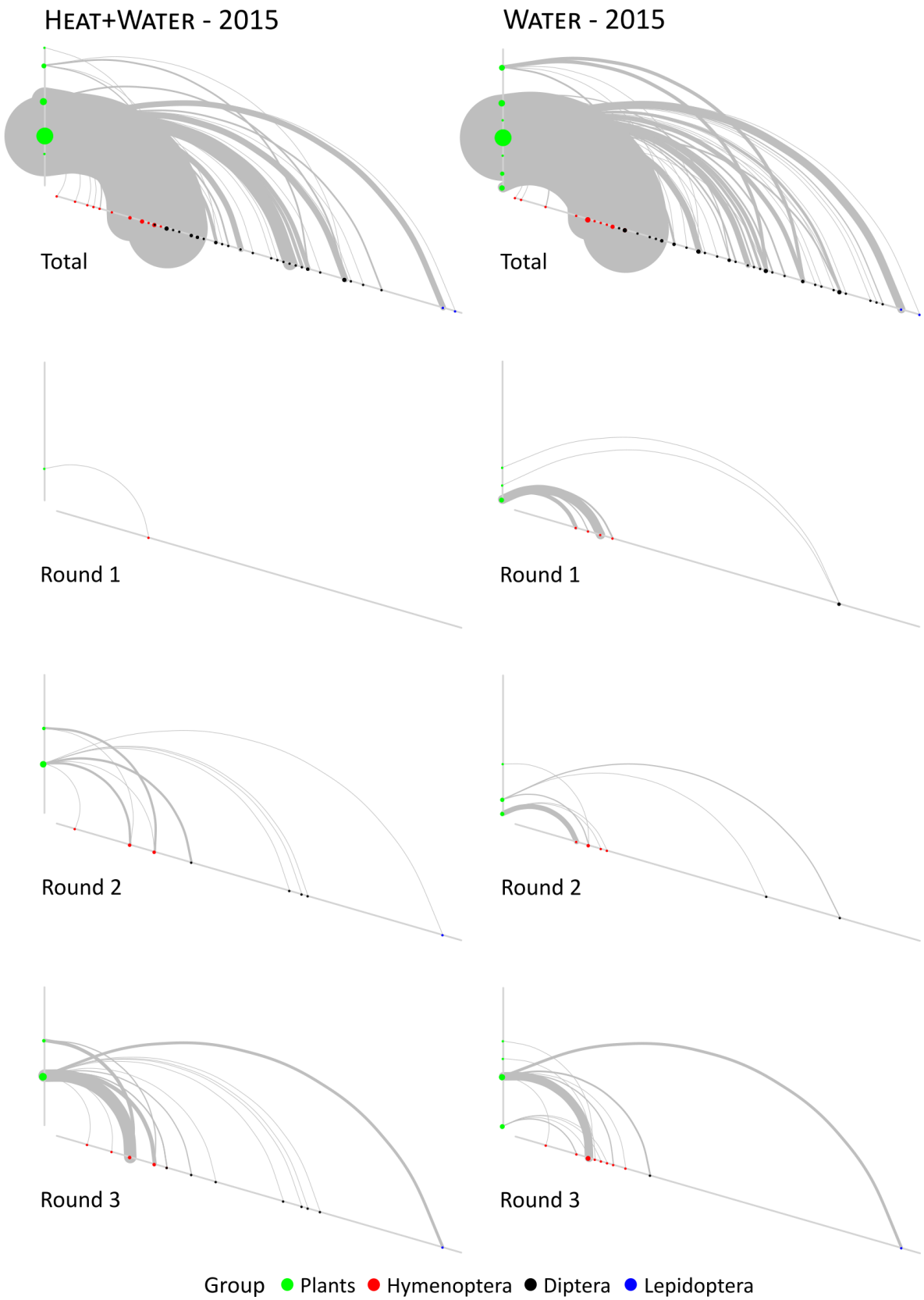

Figure 4.11 Comparison of the network structure and phenology for the combined total network and the individual temporal networks from sample rounds 1-3, from the HEAT+WATER and WATER treatments in 2015. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

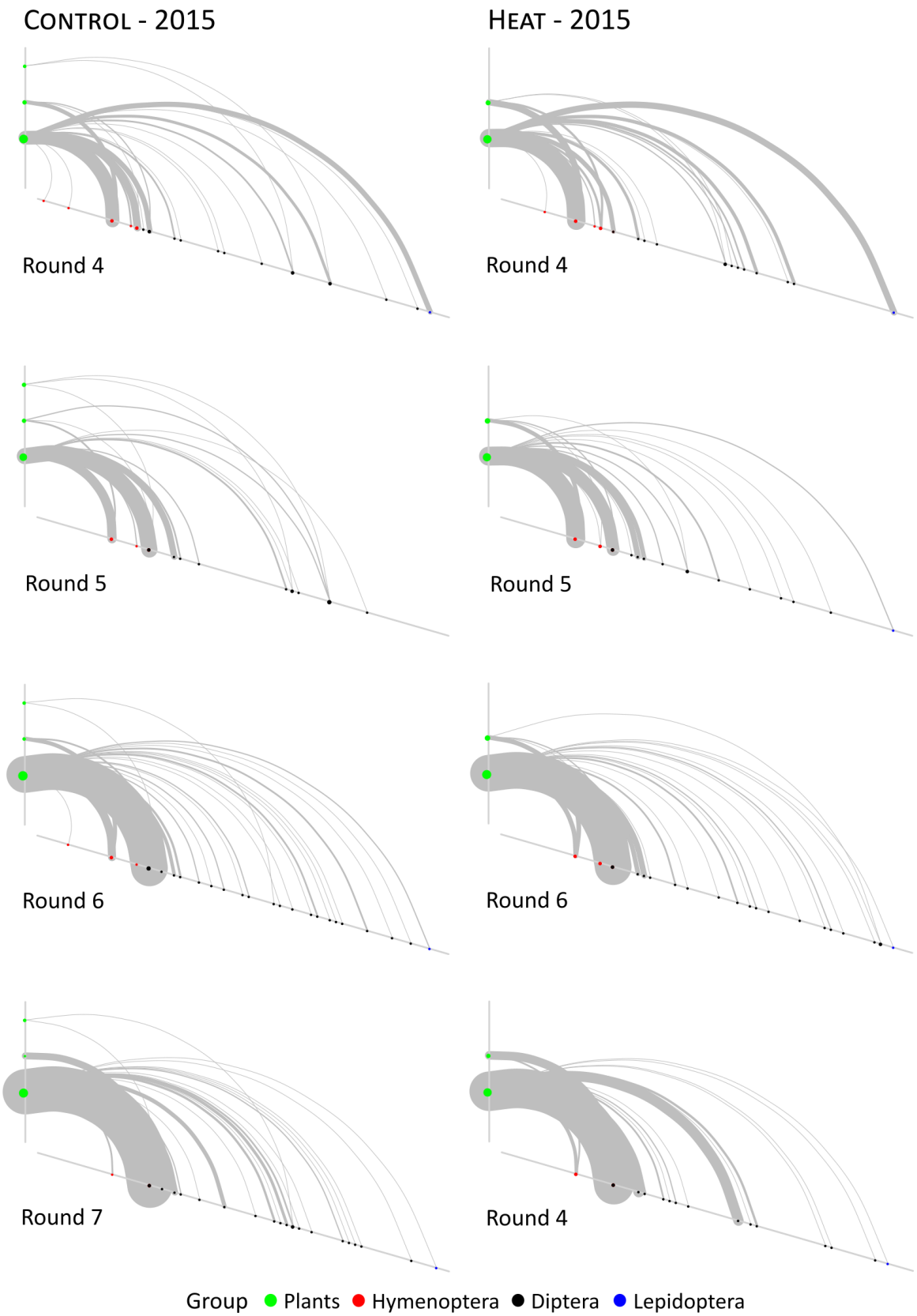

Figure 4.12 Comparison of the network structure and phenology for the individual temporal networks from sample rounds 4-7, from the CONTROL and HEAT treatments in 2015. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

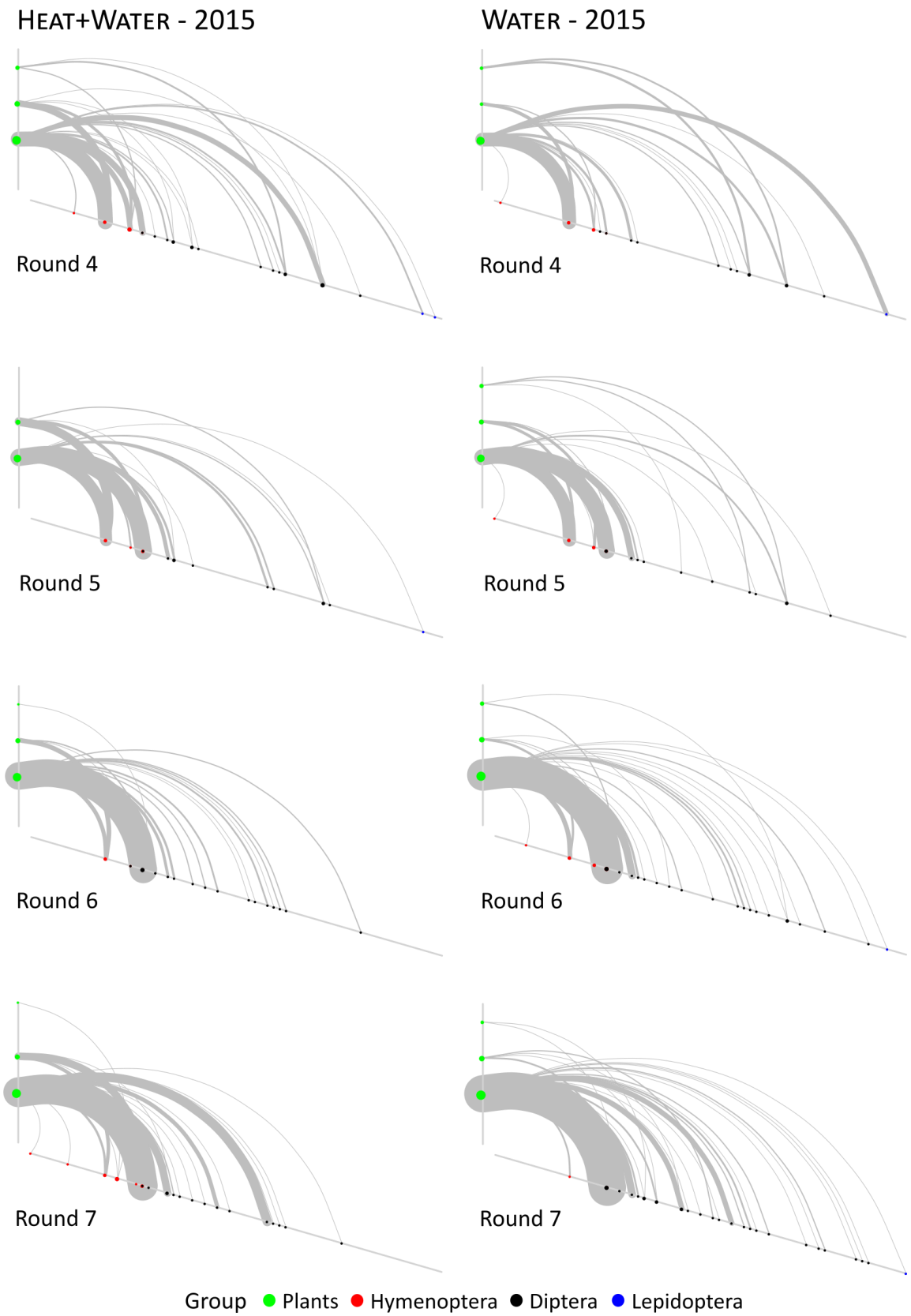

Figure 4.13 Comparison of the network structure and phenology for the individual temporal networks from sample rounds 4-7, from the HEAT+WATER and WATER treatments in 2015. Plants are on the y-axis and are ordered by date of first flowering from the total pooled network to show the plant community change through time. Insects are on the x-axis and are ordered alphabetically within each group as their phenology was not directly manipulated by our experiment.

4.4 Discussion

This study has provided the first experimental evidence of simulated warming affecting the temporal dynamics of plant-pollinator interactions both within and between years. We found that an increase of 1.5 °C was enough to cause significant reductions in floral abundance, but only in some of the sample rounds. There was also evidence that wildflower phenology was advanced by roughly one week under the warming treatments. The insect community proved to be significantly different between the two years with far more hoverflies in the first (2014). The evidence suggests that hoverflies were more susceptible to the negative impacts of the simulated warming than other insect groups, which explains why visitor richness was found to be significantly affected by treatment (in some of the sample rounds) in only 2014. We found significant temporal variation in the frequency of both total and unique interactions and significant treatment effects in some sample rounds, but the impact of the treatments was highly variable and linked to both the ambient air temperature and the composition of the insect community. Species and interaction turnover were generally high in both years and declined over the seasons, but the mechanism of interaction turnover varied greatly between the two years, with interaction rewiring being more dominant in 2014, while species turnover had a greater impact in 2015. The structure of the interaction networks was broadly similar between treatments, but it varied greatly over the course of the field seasons and there was some advancement of these structural changes seen in the heated treatments. The structure of the networks was far simpler in 2015 due to the decreased wildflower species richness.

4.4.1 Limitations

There are several limitations associated with the methodology employed in this chapter, most of which relate to the simulated warming experimental design and so are also discussed in Chapter 3 (3.4.1). Because the experiment operated at a small spatial scale, both in terms of replicate size and number, there is an increased risk that the findings may not scale-up to impacts on ecosystem processes at the landscape level and there is also an increased risk of edge effects. The linear heaters used in this simulated warming experiment restrict the plot size to 2 x 2m, and while there have been more expensive heating array demonstrations that allow for greater plot sizes (Kimball et al., 2008), other studies have simulated climate warming in situ using the same or similar heaters as they are currently the

most economically viable method (Berthe et al., 2015; Kimball, 2005; Rollinson and Kaye, 2012; Wan et al., 2005; Zhu et al., 2015). In future, experimental warming studies will need to be replicated spatially in a wide range of habitats, at larger scales where possible, and coordinated in such a way to improve meta-analyses. Another limitation associated with the methodology arises from the open-air nature of the experiment; it permitted free movement of insects in and out of the plots, which prevented direct manipulation of them with the experimental treatments. To investigate the responses of entire communities of wild pollinators in situ would either involve a prohibitive spatial scale, due to the foraging distances of flower-visiting insects, or an enclosed setup, which would constrain natural insect behaviour and exclude many species. As a result, we chose to employ a bottom-up approach, whereby we manipulated the plants directly and examined how the foraging behaviour of the insect community responded to any changes in the wildflowers, rather than inferring direct impacts upon the insects.

There are two limitations associated with the specific analytical methods employed in this chapter, both of which are caused by the high variability in sample sizes that was observed between the different sample rounds. Firstly, the species richness and interaction frequency analyses both examined the raw data rather than the Chao estimates, as they were deemed unreliable, and so we instead relied upon the rigorous and standardised sampling methodology employed to collect the data. In the case of interactions, it is questionable whether assessing sampling completeness using small and experimental spatial replicates is an appropriate method, given that the plots may have had different plant species within them during the different time points, which could result in the pool of potential interactions being drastically different between spatial replicates. This difference matters because the potential pool for each of these plots could be well represented by the sampled pool, but the sampling completeness would only recognise the difference between plots and would therefore, point to under-sampling. Additionally, this method of assessing sampling completeness does not take account of the variation in foraging behaviours, specialism, or commonness/rarity of the plants or insects, as it considers all interactions to be equal. Finally, because the sizes of some of the species interaction networks were very small, we were forced to aggregate them spatially before interaction turnover could be assessed, which meant that there was only one network for each sample round in each treatment. This pooling of data precluded any statistical comparisons of treatment effects

on interaction turnover; however, given that this research represents the first recorded attempt to investigate how climate warming may affect interaction turnover and plant-pollinator temporal dynamics, it remains a novel advancement. Additionally, the level of consistency that is displayed between both pairs of temperature treatments for the first two transitions in 2015, provides at least a small increase in confidence for those observed effects.

4.4.2 Wildflowers

The floral community composition was significantly different between the two years and there was a marked reduction in species richness in the second year. This is not a finding that was expected based on the experimental design we employed, whereby the same quantities and species of annual wildflower seeds and wheat were sown in the plots each year. However, the percentage cover data in Figure 4.1 provide a clue as to why; it shows the wheat in 2015 had a far lower coverage while the most abundant wildflower species (*G. segetum*) had far greater coverage. It seems likely that in 2015 the wheat failed to establish as effectively, which allowed *G. segetum* to dominate the plots and out-compete many of the smaller species. The reason for the poorer performance of the wheat plants in 2015 is unclear, but perhaps it is linked to the management of the field site; by 2015 the experimental plots had been sown with the same cultivar of wheat for four years in a row. This is very unusual management and the farm where the experiment was conducted otherwise employed standard agricultural crop rotations to maintain healthy soils and reduce the prevalence of crop pests and pathogens.

Floral abundance was significantly decreased by simulated warming in some sample rounds, but not others. In both years, treatment effects coincide with the two peak flowering periods, which correspond to the early and later flowering species. It certainly appears that heating the wildflowers reduces their floral abundances more strongly during their peak flowering periods (see Figure 4.2), so it follows that treatment effects are not present during the transition between these two periods. The far lower floral abundance observed during the later sample rounds in 2015, is likely due to the reduced species richness and different floral community; many of the species absent in 2015 were smaller plants that produce large numbers of small flowers, which meant that the large complex flowers of *G. segetum* and *C. cyanus* made up a greater proportion of the total. The

noticeable drop in floral abundance seen at the end of the season in 2014 may be caused by the sharp drop in temperatures and increase in wind-speeds that occurred at the same time (see Figures 4.S3 and 4.S4 in appendix 4.6.2). In the previous chapter we showed that simulated warming significantly reduced floral abundance in the aggregated dataset; this was in-line with findings from both simulated warming experiments and a long-term passive project that showed climate warming can cause a reduction in the numbers of flowering plant individuals (Liu et al., 2012; Saavedra et al., 2003) and flowers per plant (Saavedra et al., 2003). There are very few experimental studies that have examined floral abundance changes in relation to climate warming and unfortunately none of them looked at abundance patterns over time.

Simulated warming advanced floral phenology by roughly one week in both years. This is seen in the timing of flowering onset, cessation, and abundance peaks (Figure 4.2). This advancement is also seen in the interaction network plots (Figures 4.6-4.13), where the losses of early species of wildflower are seen roughly one round sooner in the heated treatments. A similar rate of advanced flowering of 5.5 days per degree Celsius was also seen in another climate change study employing an experimental approach with infra-red heaters, in a subalpine habitat in the USA (Dunne et al., 2003). The phenological advancement detected in our experiment fits with observed changes in plant phenology in the UK, where long-term records have shown advancement connected to changes in temperature (Fitter and Fitter, 2002), with one analysis suggesting an increase in 2-5 days per degree Celsius (Sparks et al., 2000).

4.4.3 Flower-visitors

The composition of the flower-visiting insect community differed significantly between the two years, with hoverflies dominating the community in 2014 while bees were more numerous in 2015 (Figure 4.3). This significant change in community composition is consistent with other multi-year plant-pollinator interaction studies (Alarcón et al., 2008; Olesen et al., 2008; Petanidou et al., 2008). The considerable difference in the insect community is likely responsible for some of the other differences that were found between the two years. Treatment had a significant effect on raw species richness in some of the sample rounds in 2014, but none in 2015, suggesting that hoverflies may be more susceptible to the effects of simulated warming than bees. This could be due to a number of

factors, such as foraging behaviour, reproductive strategies, and physiology. Ambient air temperature was found to have a significant effect on species richness in 2015, but not 2014. This again could be due to the difference in the insect community, but it is likely that the generally lower air temperatures recorded in 2015 also played a role. It is possible that a colder spring in 2015 lead to a later emergence of adult hoverflies, leaving the bumblebees with less competition for the floral resources in the plots. It is also possible that insects other than bumblebees were too cold to forage during the earlier sample rounds in 2015. Regardless of the causes, the differences in community composition, responses to simulated warming, and the responses to ambient air temperature between the two years of this study, highlight the importance of collecting data from multiple years.

4.4.4 Interaction frequency

The frequency of interactions showed distinct within-season and between-year temporal dynamics. In 2014 the distributions of both total and unique interactions are very similar, with steadily increasing values for the first few sample rounds until there is a steep increase at round five, which is then followed by sharp declines (Figure 4.4). The drop-off in interactions at the end of the season in 2014 is mirrored by a similar decrease seen in floral abundance (Figure 4.2), but the reduction is seen one round sooner in the interactions. This decrease is again likely due to the sudden drop in temperatures and increase in windspeeds that occurred at the end of July and continued into August (Figures 4.S3 and 4.S4 in appendix 4.6.2), which explains why the subsequent impact was seen first in the insect foraging behaviour. The temporal interaction distributions in 2015 are different from those of 2014 and from each other. While total interactions in 2015 increased steadily throughout the season, unique interactions increased up to round four but thereafter showed very little overall change (Figure 4.4). The shapes of these two distributions can once again be linked to the floral abundance; unique interactions begin to decrease in the second half of the season in 2015, which coincides with the expansion and peak flowering of *G. segetum* (Figures 4.1 and 4.2) and its domination in the networks (Figures 4.10-4.13), while, somewhat unsurprisingly, the pattern for total interactions in 2015 follows the distribution of the *G. segetum* floral abundance as it becomes increasingly dominant.

Very few studies report on pollinator visitation throughout a field season and there are many possible methodological and statistical reasons for this, but it does mean that

there is a sparsity of research to which these findings can be compared. There is evidence of within-season fluctuations in pollinator abundance linked to floral abundances from Eckhart (1992), and evidence of a positive effect of floral abundance on pollinator visitation in Fowler et al. (2016) and Jens et al. (2009).

There were significant treatment effects upon the frequency of both total and unique interactions in some of the sample rounds, but the impact of the treatments was highly variable and linked to both the ambient air temperature and the composition of the insect community. 2014 was characterised by generally warm temperatures (until the cold snap seen at the end of the season, see Figures 4.S3 and 4.S4), high floral diversity (Table 4.1), and by a community dominated by hoverflies (Figure 4.3). This contrasts with 2015's generally cooler temperatures, lower floral diversity, and bee dominated community. Once again it appears that hoverflies were particularly susceptible to the simulated warming as the strongest effects on both unique and total interactions are seen in the latter half of the season in 2014, when their numbers are greatest, and the values in the heated treatments are significantly lower (Figure 4.4). The results from 2015 are more complicated, and show both positive and negative impacts of simulated warming on interactions, but they are weaker relationships than those in 2014. The positive effects are seen on both total and unique interactions earlier in the season when temperatures were lower and most of the visitors were bumblebees, while the negative impacts are only really seen in unique interactions in the middle of the season and towards the end of it, when the temperatures are slightly higher and the community is more mixed. This suggests that during colder periods, bumblebees were favouring the heated plots, but once temperatures had increased slightly and other species became numerous, the insect community foraged less (overall) in the heated plots.

These findings suggest that simulated warming can significantly affect species interactions both negatively and positively, and that this is mediated by the composition of the insect community and the ambient weather conditions. There is a great deal of variation amongst pollinator groups in terms of the different aspects of their life histories, including reproductive strategies, foraging behaviour, foraging requirements, diet specialism, migration, flight periods/phenophases, and environmental tolerances. It is fair to assume then, that climate change may affect these groups differently and there is some support from other studies. Aguirre-Gutiérrez et al. (2017) showed that the differing responses of

different pollinator groups to previous climate change was influenced by functional traits. Burkle et al. (2013) studied plant-pollinator interactions on the same site over a long period of time and found certain insect groups were disproportionately lost from their networks, again most likely due to differences in functional traits. The results from both the community and interaction analyses in this study, appear to suggest that hoverflies are more susceptible to simulated warming than bees. However, this conclusion could also be interpreted the other way around; bees may not have the luxury of being able to avoid sub-optimal foraging habitat, due to the increased foraging requirements and spatial restrictions that are associated with offspring provisioning, and the increased likelihood of diet specialism.

4.4.5 Interaction turnover

There is strong temporal variation seen in network structure between the sample rounds in the network diagrams (Figures 4.6-4.13). This is caused by the loss of early species of plant and insect visitor and the addition of later species. There is also strong variation in structure seen between the two years, with simpler networks observed in 2015. This is caused by the much lower values of wildflower richness and significantly different wildflower community present in 2015. Unsurprisingly there is also strong within-season and between-year variation seen in interaction turnover and the mechanisms that drive it. β_{WN} (interaction turnover) and β_S (species turnover) decreased throughout both field seasons, but remained high, suggesting that the networks became slightly more stable over time as changes in community composition and foraging behaviour reduced. Over the course of the season, the relative contributions of the two components of interaction turnover changed. In 2014 there is a gradual shift from interaction rewiring to species turnover, while in 2015 the relative importance of species turnover decreased, and rewiring was generally less important. The differences between the two years are likely due to the differences in both the plant and insect communities. The reduction in importance of rewiring that is seen in 2014, is likely due to the gradual decrease in the number of plant species visited as *G. segetum* and *C. cyanus* come to dominate the networks (Figures 4.6-4.9); insects are either feeding from these two plants in the plots or they are not feeding there. The reduced contribution of rewiring that was observed throughout 2015 is likely due to several factors: far lower wildflower species richness throughout the season in 2015, and the consequentially far simpler networks; the greater proportion of hoverflies in 2014, which

have long flight periods in UK (Stubbs and Falk, 2002); and the far greater proportion of wild bees in 2015, which tend to have shorter flight periods and more specialised diets than hoverflies (Else and Edwards, 2018).

There are several studies that have compared the structure of aggregated or single time-point plant-pollinator networks between years, and all of them find that structure to be stable across years (Alarcón et al., 2008; Dupont et al., 2009; Olesen et al., 2008; Petanidou et al., 2008). This runs contrary to our results, but these studies were conducted in semi-natural or natural habitats, whereas our field site was on a farm that was ploughed and re-sown with annuals each year. This method creates a fresh community each season, and in our case, allows farm management to impact the plant community and subsequent network structure. There is a great scarcity of studies that have examined network structure and interaction turnover throughout a season, but our findings of distinct temporal patterns support those that have. Olesen et al. (2008) created daily plant-pollinator networks in an arctic site to examine the day-to-day changes in structure throughout the season; they found high temporal variation within the seasons characterised by an increase in network complexity over time before an abrupt collapse at the end of the season. The temporal variation in their networks was driven by turnover of plant and pollinator species and also by the shorter phenophases of the species active later in the season. These findings are quite different to ours, where we found the networks became slightly more stable over time as species turnover reduced; this highlights that networks from different habitats and locations can show distinct temporal dynamics. Burkle and Alarcón (2011) conducted a small case study in their review, which investigated the impact of species turnover on interaction networks using weekly time-slices throughout a season; they found that the pattern of interactions and network topology were very closely linked to plant species turnover. CaraDonna et al. (2017) constructed weekly plant-pollinator networks in a subalpine system to assess interaction turnover throughout three field seasons. Using a very similar method to that employed in this study, they also found that both species and interaction turnover decreased throughout the seasons, and the patterns for the two contributors to interaction turnover are similar to those we observed in 2015. They found greater consistency between seasons than we did, again most likely due to the difference in system, but generally our findings support theirs and vice versa.

The structure of the interaction networks was broadly similar between treatments in both years, but there was some advancement seen in the structural changes caused by plant phenological advancement in the heated treatments (Figures 4.6-4.13). There don't appear to be any treatment effects upon interaction turnover in 2014 but we do see small peaks in species turnover at transition 3 for the WATER treatment and transition 4 for HEAT, which are mirrored in the values for the contribution of species turnover to interaction turnover (Figure 4.5). Looking at the relevant network diagrams reveals that these peaks are caused by more noticeable turnover of both plant and insect species than is seen in the other treatments at those transitions (Figures 4.6-4.9). The reasons for these effects are unclear, but as the data used for this analysis were pooled across spatial replicates (due to small sample sizes), we could not conduct statistical tests and so cannot be sure they are meaningful. The treatment effects seen in 2015 are clearer and easier to interpret. At the start of the season there is clustering of the heated and unheated treatments into two distinct patterns; the heated treatments show very high species and interaction turnover in the first transition, which then drops dramatically in the second, while the unheated ones show lower values initially followed by a more gradual increase. After the third transition the differences even out and all treatments gradually decrease. The same pattern of treatment effects is seen in the contribution of species turnover to interaction turnover, but rewiring shows little by way of treatment effects. Again, looking at the network diagrams suggests these patterns are linked to the phenological advancement of the plants under simulated warming, and that the effect may be magnified by the already low wildflower species richness. These findings also suggest that the effects of the simulated warming on interaction turnover are mediated by insect community composition, given that the only instance of clear and strong treatment effects coincided with the only instance of wild bees dominating the insect community composition. This mediation likely occurs via the more restricted flight periods and diet specialisations possessed by wild bees when compared to hoverflies, which is especially pronounced for long-tongued species (like *B. hortorum*) that are adapted to feed from flowers with a long corolla (like that of *L. purpureum*) (Else and Edwards, 2018; Stubbs and Falk, 2002).

We have demonstrated that plant-pollinator network structure may not be consistent between years in arable agro-ecosystems. Previous studies have all confirmed invariant network structure despite high species turnover in semi-natural habitats with

persistent vegetation communities (Alarcón et al., 2008; Dupont et al., 2009; Olesen et al., 2008; Petanidou et al., 2008), but we can no longer extrapolate from this established finding and assume that network structure is stable over multiple years in habitats that experience significant change. Our findings indicate that temporal plant-pollinator network structure is consistent across climate change treatments, but at key seasonal transitions in the plant community, phenological advancement is apparent. We have also shown that simulated warming could affect species and interaction turnover, and again this is most likely via phenological advancement. At present there are few studies whose results these findings can support and vice versa. There is plenty of evidence demonstrating that climate change causes phenological advancement (Dunne et al., 2003; Fitter and Fitter, 2002; Sparks et al., 2000), and that this can disrupt plant-pollinator interactions (Burkle et al., 2013; Kudo and Ida, 2013; Memmott et al., 2007). We also now have sufficient evidence to state that plant-pollinator networks exhibit significant within-season temporal dynamics (CaraDonna et al., 2017; Olesen et al., 2008), and that these dynamics are likely to be disrupted by changes in plant and insect phenology and abundances that are caused by climate change (Burkle and Alarcón, 2011). Our findings also support the suggestion by Burkle and Alarcón (2011) that the smaller temporal scales used to examine intra-annual interaction dynamics are more appropriate for the temporal scales associated with climate-warming induced phenology advancements, than aggregated or single time-point interaction networks.

In conclusion, our findings display distinct within-season temporal dynamics in wildflower floral abundance and plant-pollinator interactions that are obscured when the data are pooled across time. Our results also demonstrate that these dynamics can be disrupted by simulated climate warming, but the nature of the disruption is mediated by insect community composition, flowering phenology, and ambient weather conditions. Our study highlights the need for a more detailed approach to interaction studies that incorporates analyses of within-season temporal fluctuations in both network structure and interaction turnover, especially in relation to climate change. The considerable inter-annual variation that was displayed across all datasets further highlights the need for longer-term studies.

4.5 References

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4.6 Appendix

Sampling Completeness: Insect Species

Year	Round	Treatment	Species Richness	Chao Estimate	Proportion detected	Year	Round	Treatment	Species Richness	Chao Estimate	Proportion detected
2014	1	All	24	51.0 ± 20.1	47.1	2015	1	All	11	28.3 ± 22.7	38.9
	2	All	18	18.4 ± 0.8	97.9		2	All	21	50.0 ± 27.5	42.0
	3	All	24	30.5 ± 5.7	78.8		3	All	21	30.7 ± 8.7	68.4
	4	All	36	53.5 ± 11.8	67.3		4	All	31	40.7 ± 7.7	76.2
	5	All	54	113.9 ± 36.8	47.4		5	All	24	31.8 ± 8.0	75.4
	6	All	27	31.7 ± 4.7	85.2		6	All	35	40.1 ± 4.7	87.3
	7	All	31	47.0 ± 14.2	66.0		7	All	39	57.0 ± 12.6	68.5
2014	1	Control	11	21.2083 ± 11.0391	51.9	2015	1	Control	5	6.6667 ± 3.1623	75.0
	2	Control	14	15.1111 ± 1.5973	92.6		2	Control	7	17.4167 ± 14.3433	40.2
	3	Control	14	15.1111 ± 1.5973	92.6		3	Control	9	24 ± 19.7484	37.5
	4	Control	25	37 ± 9.4234	67.6		4	Control	19	32.8889 ± 12.4639	57.8
	5	Control	30	51.3333 ± 15.0377	58.4		5	Control	13	13.9375 ± 1.5261	93.3
	6	Control	19	35.875 ± 16.9062	53.0		6	Control	26	37.7361 ± 8.7791	68.9
	7	Control	21	26.625 ± 4.9961	78.9		7	Control	22	30.4028 ± 6.7709	72.4
2014	1	Heat	8	25.5 ± 14.3713	31.4	2015	1	Heat	6	14.3333 ± 8.4306	41.9
	2	Heat	10	13.4722 ± 4.1396	74.2		2	Heat	13	46.75 ± 40.9764	27.8
	3	Heat	13	18.2083 ± 6.3618	71.4		3	Heat	9	10.875 ± 2.8845	82.8
	4	Heat	15	17.6042 ± 3.1185	85.2		4	Heat	18	21.75 ± 4.0793	82.8
	5	Heat	28	34.6667 ± 5.1400	80.8		5	Heat	16	21 ± 5.4772	76.2
	6	Heat	17	30.3333 ± 13.8243	56.0		6	Heat	22	30.3333 ± 7.0711	72.5
	7	Heat	15	56.6667 ± 49.7215	26.5		7	Heat	17	43.6667 ± 33.0656	38.9
2014	1	Heat+Water	15	85.4167 ± 80.9606	17.6	2015	1	Heat+Water	2	2 ± 0.2946	100.0
	2	Heat+Water	14	20.6667 ± 6.3246	67.7		2	Heat+Water	9	19.4167 ± 14.3433	46.4
	3	Heat+Water	17	23.6667 ± 6.3246	71.8		3	Heat+Water	14	27.3333 ± 13.8243	51.2
	4	Heat+Water	17	33.875 ± 16.9062	50.2		4	Heat+Water	19	27.4375 ± 7.6076	69.2
	5	Heat+Water	22	57.2083 ± 32.1939	38.5		5	Heat+Water	13	15.2222 ± 2.9676	85.4
	6	Heat+Water	14	16.0833 ± 2.5345	87.0		6	Heat+Water	19	25.6667 ± 6.3246	74.0
	7	Heat+Water	18	28.4167 ± 8.9970	63.3		7	Heat+Water	21	91.4167 ± 80.9606	23.0
2014	1	Water	5	8.75 ± 6.0467	57.1	2015	1	Water	6	7.6667 ± 3.1623	78.3
	2	Water	10	15.2083 ± 6.3618	65.8		2	Water	7	10.75 ± 6.0467	65.1
	3	Water	8	9.6667 ± 3.1623	82.8		3	Water	11	18.5 ± 8.5513	59.5
	4	Water	16	29.3333 ± 13.8243	54.5		4	Water	16	26.2083 ± 11.0391	61.0
	5	Water	34	45.7188 ± 8.0936	74.4		5	Water	15	35.4167 ± 25.9895	42.4
	6	Water	18	59.6667 ± 49.7215	30.2		6	Water	24	32.4028 ± 6.7709	74.1
	7	Water	21	27.75 ± 6.0094	75.7		7	Water	26	36 ± 7.7460	72.2

Table 4.S2 Insect richness sampling completeness. Number of flower visitors recorded per sampling round for both years in each treatment seperately and all treatments combined, with estimated values and estimated proportion detected. Chao estimates are given with standard errors.

Year	Round	Treatment	Unique Interactions	Chao Estimate	Proportion detected	Year	Round	Treatment	Unique Interactions	Chao Estimate	Proportion detected
2014	1	All	33	220.8 ± 151.2	14.9	2015	1	All	13	28.3 ± 15.8	45.9
	2	All	52	78.8 ± 13.5	66.0		2	All	28	58.7 ± 22.4	47.7
	3	All	56	118.1 ± 29.6	47.4		3	All	26	43.3 ± 13.8	60.1
	4	All	55	89.2 ± 17.5	61.7		4	All	42	76.6 ± 22.9	54.8
	5	All	85	184.8 ± 41.6	46.0		5	All	35	46.5 ± 8.8	75.3
	6	All	46	101.2 ± 34.2	45.5		6	All	45	54.0 ± 6.6	83.3
	7	All	46	123.3 ± 56.2	37.3		7	All	51	93.8 ± 24.4	54.4
2014	1	Control	12	45.75 ± 40.9764	26.2	2015	1	Control	5	6.6667 ± 3.1623	75.0
	2	Control	25	45.0694 ± 13.4897	55.5		2	Control	7	17.4167 ± 14.3433	40.2
	3	Control	26	227.667 ± 219.6942	11.4		3	Control	10	30.4167 ± 25.9895	32.9
	4	Control	33	66.6111 ± 20.6712	49.5		4	Control	24	70.875 ± 41.6106	33.9
	5	Control	36	66.625 ± 19.1203	54.0		5	Control	19	24.3333 ± 5.0244	78.1
	6	Control	26	153.5 ± 61.9427	16.9		6	Control	29	44.625 ± 11.0190	65.0
	7	Control	26	39.6111 ± 9.8702	65.6		7	Control	25	35.0595 ± 7.4601	71.3
2014	1	Heat	8	25.5 ± 14.3713	31.4	2015	1	Heat	6	14.3333 ± 8.4306	41.9
	2	Heat	15	45 ± 27.9285	33.3		2	Heat	15	35.8333 ± 20.2844	41.9
	3	Heat	25	70 ± 34.2053	35.7		3	Heat	11	14.3333 ± 4.4721	76.7
	4	Heat	20	30.4167 ± 8.9970	65.8		4	Heat	21	32.25 ± 10.4732	65.1
	5	Heat	34	52.8021 ± 11.7225	64.4		5	Heat	21	31.4167 ± 8.9970	66.8
	6	Heat	21	34.8889 ± 12.4639	60.2		6	Heat	27	45.75 ± 13.5208	59.0
	7	Heat	18	88.4167 ± 80.9606	20.4		7	Heat	20	53.75 ± 40.9764	37.2
2014	1	Heat+Water	16	103.5 ± 46.8261	15.5	2015	1	Heat+Water	2	2 ± 0.2946	100.0
	2	Heat+Water	23	198 ± 78.3142	11.6		2	Heat+Water	11	31.4167 ± 25.9895	35.0
	3	Heat+Water	24	50.6667 ± 19.5505	47.4		3	Heat+Water	16	24.8889 ± 8.6448	64.3
	4	Heat+Water	25	51.6667 ± 19.5505	48.4		4	Heat+Water	27	40.6111 ± 9.8702	66.5
	5	Heat+Water	26	52.6667 ± 19.5505	49.4		5	Heat+Water	17	20.75 ± 4.0793	81.9
	6	Heat+Water	19	27.3333 ± 7.0711	69.5		6	Heat+Water	23	29.9444 ± 5.8542	76.8
	7	Heat+Water	23	49.6667 ± 19.5505	46.3		7	Heat+Water	26	139.3333 ± 56.7744	18.7
2014	1	Water	6	12.6667 ± 9.7753	47.4	2015	1	Water	7	10.75 ± 6.0467	65.1
	2	Water	19	50.25 ± 24.8433	37.8		2	Water	8	11.3333 ± 4.4721	70.6
	3	Water	14	47.75 ± 40.9764	29.3		3	Water	14	30.875 ± 16.9062	45.3
	4	Water	23	46.4375 ± 17.5286	49.5		4	Water	20	24.0833 ± 4.1165	83.0
	5	Water	54	135.488 ± 41.8088	39.9		5	Water	20	40.8333 ± 20.2844	49.0
	6	Water	24	130.667 ± 119.7033	18.4		6	Water	31	50.2857 ± 12.4528	61.6
	7	Water	27	53.6667 ± 19.5505	50.3		7	Water	32	51.2857 ± 12.4528	62.4

Table 4.S3 Interactions sampling completeness. Number of Unique interactions recorded per sampling round for both years in each treatment seperately and all treatments combined, with estimated values and estimated proportion detected. Chao estimates are given with standard errors.

Floral abundance 2014					Floral abundance 2015				Floral richness 2014				Floral richness 2015			
Model Summary					**Model Summary**				**Model Summary**				**Model Summary**			
	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**
(Intercept)	5.2692	0.1440	36.6	*< 2e-16*	5.3364	0.1437	37.14	*< 2e-16*	1.9310	0.0586	32.95	*< 2e-16*	1.3816	0.0771	17.925	*< 2e-16*
TreatmentHeat	-0.5956	0.2039	-2.92	*0.0035*	-0.2215	0.2032	-1.09	0.2758	-0.1667	0.0863	-1.93	0.0533	-0.2202	0.1143	-1.926	0.0541
TreatmentHeat+Water	-0.5453	0.2039	-2.67	*0.0075*	-0.3618	0.2033	-1.78	0.0752	-0.1350	0.0856	-1.58	0.1146	-0.0661	0.1097	-0.602	0.5469
TreatmentWater	-0.2069	0.2037	-1.02	0.3098	0.1485	0.2031	0.73	0.4646	-0.0781	0.0843	-0.93	0.3544	0.0230	0.1073	0.214	0.8303
Round.L	0.2416	0.1224	1.97	*0.0485*	-0.1343	0.1383	-0.97	0.3316	-0.1555	0.0855	-1.82	0.0689	-0.4330	0.1022	-4.239	*<0.0001*
Round.Q	0.3002	0.1244	2.41	*0.0158*	1.0454	0.1378	7.59	*<0.0001*	-0.2740	0.0848	-3.23	*0.0012*	0.2617	0.1077	2.429	*0.0151*
Round.C	-0.5095	0.1232	-4.14	*<0.0001*	-0.5691	0.1377	-4.13	*<0.0001*	0.1229	0.0824	1.49	0.1358	0.1121	0.1031	1.088	0.2767
Round^4	-0.8521	0.1229	-6.93	*<0.0001*	-0.3519	0.1379	-2.55	*0.0107*	-0.0854	0.0805	-1.06	0.2885	-0.2321	0.1092	-2.125	*0.0336*
Round^5	0.3898	0.1222	3.19	*0.0014*	0.6012	0.1396	4.31	*<0.0001*	-0.1917	0.0792	-2.42	*0.0155*	0.1236	0.1040	1.188	0.2347
Round^6	0.2684	0.1241	2.16	*0.0306*	-0.2453	0.1395	-1.76	0.0787	0.0104	0.0787	0.13	0.8945	0.2446	0.1153	2.122	*0.0339*
TreatmentHeat:Round.L	-0.2555	0.1761	-1.45	0.1467	0.6551	0.1977	3.31	*0.0009*	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round.L	-0.3887	0.1753	-2.22	*0.0266*	0.4852	0.1974	2.46	*0.0140*	-	-	-	-	-	-	-	-
TreatmentWater:Round.L	0.3360	0.1746	1.92	0.0543	-0.2593	0.1955	-1.33	0.1848	-	-	-	-	-	-	-	-
TreatmentHeat:Round.Q	-0.0623	0.1773	-0.35	0.7255	-0.9727	0.1953	-4.98	*<0.0001*	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round.Q	0.0742	0.1770	0.42	0.6750	-0.6520	0.1961	-3.32	*0.0009*	-	-	-	-	-	-	-	-
TreatmentWater:Round.Q	-0.0438	0.1764	-0.25	0.8039	0.1730	0.1949	0.89	0.3747	-	-	-	-	-	-	-	-
TreatmentHeat:Round.C	-0.1361	0.1759	-0.77	0.4392	0.2488	0.1954	1.27	0.2029	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round.C	-0.1094	0.1762	-0.62	0.5348	0.1574	0.1957	0.8	0.4213	-	-	-	-	-	-	-	-
TreatmentWater:Round.C	-0.1463	0.1744	-0.84	0.4015	-0.0009	0.1948	0	0.9962	-	-	-	-	-	-	-	-
TreatmentHeat:Round^4	0.8116	0.1761	4.61	*<0.0001*	0.5537	0.1958	2.83	*0.0047*	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round^4	0.6520	0.1760	3.71	*0.0002*	0.5042	0.1960	2.57	*0.0101*	-	-	-	-	-	-	-	-
TreatmentWater:Round^4	0.2640	0.1741	1.52	0.1295	0.0449	0.1943	0.23	0.8174	-	-	-	-	-	-	-	-
TreatmentHeat:Round^5	-0.6488	0.1751	-3.71	*0.0002*	-0.4300	0.1974	-2.18	*0.0293*	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round^5	-0.5232	0.1754	-2.98	*0.0029*	-0.5844	0.1972	-2.96	*0.0030*	-	-	-	-	-	-	-	-
TreatmentWater:Round^5	-0.1165	0.1737	-0.67	0.5023	0.0068	0.1964	0.03	0.9722	-	-	-	-	-	-	-	-
TreatmentHeat:Round^6	0.0156	0.1770	0.09	0.9297	0.0410	0.1966	0.21	0.8347	-	-	-	-	-	-	-	-
TreatmentHeat+Water:Round^6	-0.2561	0.1773	-1.44	0.1486	0.3444	0.1973	1.75	0.0808	-	-	-	-	-	-	-	-
TreatmentWater:Round^6	-0.1068	0.1761	-0.61	0.5445	0.0447	0.1972	0.23	0.8208	-	-	-	-	-	-	-	-
Analysis of Variance Table					**Analysis of Variance Table**				**Analysis of Variance Table**				**Analysis of Variance Table**			
	Df	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**
Treatment	3	11.781	3.9271	3.9271	3	7.891	2.6304	2.6304	3	4.3901	1.4634	1.4634	3	5.371	1.7904	1.7904
Round	6	181.369	30.2282	30.2282	6	173.194	28.8657	28.8657	6	25.0139	4.169	4.169	6	35.572	5.9287	5.9287
Treatment:Round	18	69.935	3.8853	3.8853	18	108.267	6.0148	6.0148	-	-	-	-	-	-	-	-
Single term deletions					**Single term deletions**				**Single term deletions**				**Single term deletions**			
	Df	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**
Treatment	-	-	-	-	-	-	-	-	3	707.67	4.29	0.2318	3	632.61	4.99	0.1725
Round	-	-	-	-	-	-	-	-	6	722.15	24.771	*0.0004*	6	657.76	36.14	*<0.0001*
Treatment:Round	18	1874.4	69.393	*<0.0001*	18	2034.2	103.54	*<0.0001*	-	-	-	-	-	-	-	-

Table 4.S4 GLMM results for floral abundance and floral richness in 2014 and 2015, showing the effect of treatment, sample round and a treatment:round interaction . The interaction was not significant for floral richness in 2014 or 2015, so it was dropped from the final model. Model outputs are taken directly from R using the following functions: summary(), anova(test="Chisq"), drop1(test="Chisq"). Significant p values (p<0.05) are shown in italic.

GLMM Table: Insect Data

Visitor richness 2014					Visitor richness 2015			
Model Summary					**Model Summary**			
	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**
(Intercept)	1.7435	0.0687	25.376	*< 2e-16*	0.3241	0.4792	0.6760	0.4989
TreatmentHeat	-0.3113	0.1092	-2.85	*0.0044*	0.1614	0.1035	1.5600	0.1187
TreatmentHeat+Water	-0.2079	0.1007	-2.066	*0.0388*	0.0932	0.1053	0.8850	0.3763
TreatmentWater	-0.3100	0.1143	-2.712	*0.0067*	0.1673	0.1020	1.6400	0.1010
Round.L	1.0108	0.2031	4.976	*<0.0001*	1.6659	0.1411	11.8070	*< 2e-16*
Round.Q	-0.6486	0.1952	-3.323	*0.0009*	-0.6686	0.1296	-5.1600	*<0.0001*
Round.C	-0.1655	0.1877	-0.882	0.3778	0.0884	0.1309	0.6760	0.4992
Round^4	0.0437	0.1729	0.253	0.8005	0.1641	0.1205	1.3620	0.1730
Round^5	0.4017	0.1708	2.352	*0.0187*	-0.1925	0.1252	-1.5370	0.1242
Round^6	-0.1103	0.1569	-0.703	0.4819	-0.2938	0.0962	-3.0530	*0.0023*
Temp	-	-	-	-	0.0550	0.0265	2.0730	*0.0382*
TreatmentHeat:Round.L	0.2467	0.3378	0.73	0.4652	-	-	-	-
TreatmentHeat+Water:Round.L	-0.4310	0.2950	-1.461	0.1440	-	-	-	-
TreatmentWater:Round.L	0.8583	0.3571	2.404	*0.0162*	-	-	-	-
TreatmentHeat:Round.Q	-0.4622	0.3206	-1.442	0.1494	-	-	-	-
TreatmentHeat+Water:Round.Q	0.0739	0.2824	0.262	0.7935	-	-	-	-
TreatmentWater:Round.Q	-0.2612	0.3425	-0.763	0.4456	-	-	-	-
TreatmentHeat:Round.C	0.0436	0.2987	0.146	0.8840	-	-	-	-
TreatmentHeat+Water:Round.C	0.1615	0.2729	0.592	0.5540	-	-	-	-
TreatmentWater:Round.C	0.1259	0.3135	0.401	0.6881	-	-	-	-
TreatmentHeat:Round^4	-0.0671	0.2775	-0.242	0.8090	-	-	-	-
TreatmentHeat+Water:Round^4	0.0362	0.2611	0.139	0.8897	-	-	-	-
TreatmentWater:Round^4	-0.1046	0.2797	-0.374	0.7084	-	-	-	-
TreatmentHeat:Round^5	-0.2933	0.2536	-1.157	0.2474	-	-	-	-
TreatmentHeat+Water:Round^5	-0.3784	0.2489	-1.52	0.1285	-	-	-	-
TreatmentWater:Round^5	0.2043	0.2629	0.777	0.4370	-	-	-	-
TreatmentHeat:Round^6	0.3702	0.2318	1.597	0.1102	-	-	-	-
TreatmentHeat+Water:Round^6	0.2477	0.2325	1.065	0.2868	-	-	-	-
TreatmentWater:Round^6	0.2568	0.2413	1.064	0.2874	-	-	-	-
Analysis of Variance Table					**Analysis of Variance Table**			
	Df	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**
Treatment	3	15.519	5.1731	5.1731	3	3.056	1.019	1.0185
Round	6	151.592	25.2654	25.2654	6	189.89	31.648	31.6483
Temp	-	-	-	-	1	4.362	4.362	4.3624
Treatment:Round	18	28.761	1.5978	1.5978	-	-	-	-
Single term deletions					**Single term deletions**			
	Df	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**
Treatment	-	-	-	-	3	675.18	3.262	0.3530
Round	-	-	-	-	6	910.5	244.578	*<0.0001*
Temp	-	-	-	-	1	680.28	4.353	*0.0370*
Treatment:Round	18	742.13	29.834	*0.0391*	-	-	-	-

Table 4.S5 GLMM results for visitor richness in 2014 and 2015, showing the effect of treatment, sample round, air temperature, and a treatment:round interaction. The interaction was not significant for visitor richness in 2015 and temperature was not significant in 2014, so these were dropped from the final models. Model outputs are taken directly from R using the following functions: summary(), anova(test="Chisq"), drop1(test="Chisq"). Significant p values (p<0.05) are shown in italic.

Total interactions 2014					Total interactions 2015				Unique interactions 2014				Unique interactions 2015			
Model Summary					**Model Summary**				**Model Summary**				**Model Summary**			
	Estimate	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**	**Estimate**	**Std. error**	**z value**	**Pr(>|z|)**
(Intercept)	1.4751	0.3369	4.378	*<0.0001*	1.0846	0.4203	2.581	*0.0099*	1.4827	0.0808	18.35	*< 2e-16*	-0.5245	0.6318	-0.8300	0.4064
TreatmentHeat	-0.4046	0.1355	-2.986	*0.0028*	0.2485	0.1570	1.583	0.1135	-0.2978	0.1251	-2.381	*0.0172*	0.0749	0.1501	0.4990	0.6178
TreatmentHeat+Water	-0.2366	0.1278	-1.852	0.0640	-0.0416	0.2047	-0.203	0.8389	-0.2709	0.1211	-2.237	*0.0253*	-0.1235	0.1968	-0.6280	0.5303
TreatmentWater	-0.2346	0.1337	-1.755	0.0792	0.3168	0.1500	2.111	*0.0348*	-0.1992	0.1241	-1.605	0.1085	0.2521	0.1432	1.7600	0.0783
Round.L	1.5265	0.1836	8.312	*<0.0001*	2.7411	0.2460	11.142	*<0.0001*	0.1946	0.2311	0.842	0.3998	1.1471	0.3263	3.515	*0.0004*
Round.Q	-0.8999	0.1828	-4.922	*<0.0001*	-0.4043	0.2089	-1.935	0.0530	-0.8896	*0.2112*	-4.211	*<0.0001*	-0.7434	0.2781	-2.6730	*0.0075*
Round.C	-0.3754	0.1607	-2.336	*0.0195*	-0.6110	0.2389	-2.558	*0.0105*	0.1213	*0.2133*	0.569	0.5697	-0.3217	0.3137	-1.0260	0.3050
Round^4	-0.3762	0.1405	-2.678	*0.0074*	0.6531	0.2422	2.697	*0.0070*	0.3866	0.2111	1.831	0.0671	0.7085	0.3155	2.2460	*0.0247*
Round^5	0.5098	0.1304	3.91	*0.0001*	-0.4005	0.2363	-1.695	0.0901	0.8103	0.1939	4.18	*<0.0001*	-0.6684	0.3120	-2.1420	*0.0322*
Round^6	0.0434	0.1280	0.339	0.7346	-0.4721	0.1762	-2.68	*0.0074*	0.1014	0.1666	0.609	0.5428	-0.4773	0.2330	-2.0490	*0.0405*
Temp	0.0443	0.0189	2.351	*0.0187*	0.0504	0.0230	2.194	*0.0282*	-	-	-	-	0.0821	0.0352	2.3330	*0.0196*
TreatmentHeat:Round.L	0.2155	0.3122	0.69	0.4901	-0.0799	0.3592	-0.223	0.8239	0.3094	0.3761	0.823	0.4107	-0.6325	0.4583	-1.38	0.1676
TreatmentHeat+Water:Round.L	-0.6036	0.2661	-2.269	*0.0233*	0.8648	0.6316	1.369	0.1709	-0.5785	0.3511	-1.648	0.0994	0.4802	0.6800	0.706	0.4800
TreatmentWater:Round.L	0.6339	0.3017	2.101	*0.0356*	-0.9640	0.2968	-3.248	*0.0012*	0.8634	0.3695	2.337	*0.0194*	-0.3221	0.4046	-0.796	0.4259
TreatmentHeat:Round.Q	-0.4095	0.2966	-1.381	0.1673	-0.6834	0.3264	-2.094	*0.0363*	-0.4525	0.3481	-1.3	0.1936	-0.4426	0.4216	-1.05	0.2938
TreatmentHeat+Water:Round.Q	-0.0844	0.2583	-0.327	0.7437	-1.8491	0.5953	-3.106	*0.0019*	-0.0144	0.3249	-0.044	0.9645	-1.1612	0.6378	-1.821	0.0687
TreatmentWater:Round.Q	0.0235	0.2939	0.08	0.9362	0.3814	0.2614	1.459	0.1446	-0.1394	0.3435	-0.406	0.6848	0.5453	0.3538	1.541	0.1233
TreatmentHeat:Round.C	0.3006	0.2641	1.138	0.2551	0.9211	0.3203	2.876	*0.0040*	-0.0533	0.3315	-0.161	0.8722	0.7348	0.4153	1.769	0.0769
TreatmentHeat+Water:Round.C	0.3165	0.2327	1.36	0.1738	1.5890	0.4939	3.218	*0.0013*	-0.0487	0.3193	-0.152	0.8788	1.6676	0.5534	3.014	*0.0026*
TreatmentWater:Round.C	0.3515	0.2561	1.372	0.1700	0.0966	0.2902	0.333	0.7394	0.0749	0.3300	0.227	0.8205	0.1974	0.3964	0.498	0.6185
TreatmentHeat:Round^4	0.4333	0.2336	1.855	0.0636	-0.5914	0.3002	-1.97	*0.0488*	-0.2690	0.3241	-0.83	0.4066	-0.8347	0.3906	-2.137	*0.0326*
TreatmentHeat+Water:Round^4	0.1627	0.2046	0.795	0.4265	-0.8098	0.3785	-2.139	*0.0324*	-0.2583	0.3177	-0.813	0.4162	-0.8457	0.4536	-1.864	0.0623
TreatmentWater:Round^4	0.0927	0.2176	0.426	0.6701	-0.2210	0.2997	-0.737	0.4609	-0.1680	0.3168	-0.53	0.5960	0.0564	0.4087	0.138	0.8903
TreatmentHeat:Round^5	-0.4882	0.2033	-2.401	*0.0164*	0.3564	0.2770	1.287	0.1981	-0.5069	0.2800	-1.811	0.0702	0.7278	0.3690	1.972	*0.0486*
TreatmentHeat+Water:Round^5	-0.5094	0.1877	-2.714	*0.0067*	0.4237	0.2966	1.429	0.1531	-0.5083	0.2841	-1.789	0.0736	0.6647	0.3864	1.72	0.0854
TreatmentWater:Round^5	0.2187	0.1994	1.097	0.2726	0.1549	0.2873	0.539	0.5897	0.1781	0.2851	0.625	0.5321	0.2256	0.3924	0.575	0.5654
TreatmentHeat:Round^6	0.1270	0.1839	0.69	0.4899	0.1568	0.2248	0.697	0.4855	0.4497	0.2485	1.81	0.0704	0.2317	0.3126	0.741	0.4585
TreatmentHeat+Water:Round^6	-0.0503	0.1792	-0.281	0.7791	0.3614	0.2265	1.595	0.1107	0.2078	0.2539	0.818	0.4132	0.3744	0.3143	1.191	0.2336
TreatmentWater:Round^6	0.1201	0.1924	0.624	0.5324	0.3397	0.2328	1.459	0.1446	0.2484	0.2511	0.989	0.3225	0.2263	0.3138	0.721	0.4708
Analysis of Variance Table					**Analysis of Variance Table**				**Analysis of Variance Table**				**Analysis of Variance Table**			
	Df	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**	**Df**	**Sum sq**	**Mean Sq**	**F value**
Treatment	3	22.32	7.439	7.4392	3	1.37	0.457	0.4574	3	14.887	4.9624	4.9624	3	2.73	0.91	0.91
Round	6	493.65	82.276	82.2756	6	488.98	81.496	81.4963	6	161.83	26.9717	26.9717	6	46.245	7.7076	7.7076
Temp	1	5.67	5.671	5.6709	1	5.32	5.324	5.3244	-	-	-	-	1	8.454	8.4542	8.4542
Treatment:Round	18	63.86	3.548	3.5477	18	48.14	2.675	2.6746	18	34.352	1.9085	1.9085	18	32.944	1.8302	1.8302
Single term deletions					**Single term deletions**				**Single term deletions**				**Single term deletions**			
	Df	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**	**Df**	**AIC**	**LRT**	**Pr(Chi)**
Treatment	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Round	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Temp	1	959.11	5.553	*0.0185*	1	970.5	4.825	*0.0280*	-	-	-	-	1	667.04	5.462	*0.0194*
Treatment:Round	18	984.85	65.294	*<0.0001*	18	995.61	63.94	*<0.0001*	18	760.93	35.358	*0.0085*	18	666.11	38.541	*0.0033*

Table 4.S6 GLMM results for Total and Unique interactions in 2014 and 2015, showing the effect of treatment, sample round, air temperature, and a treatment:round interaction . Temperature was not significant for Unique interactions in 2014, so it was dropped from the final model. Model outputs are taken directly from R using the following functions: summary(), anova(test="Chisq"), drop1(test="Chisq"). Significant p values (p<0.05) are shown in italic.

Betalink Output using β_{sim}

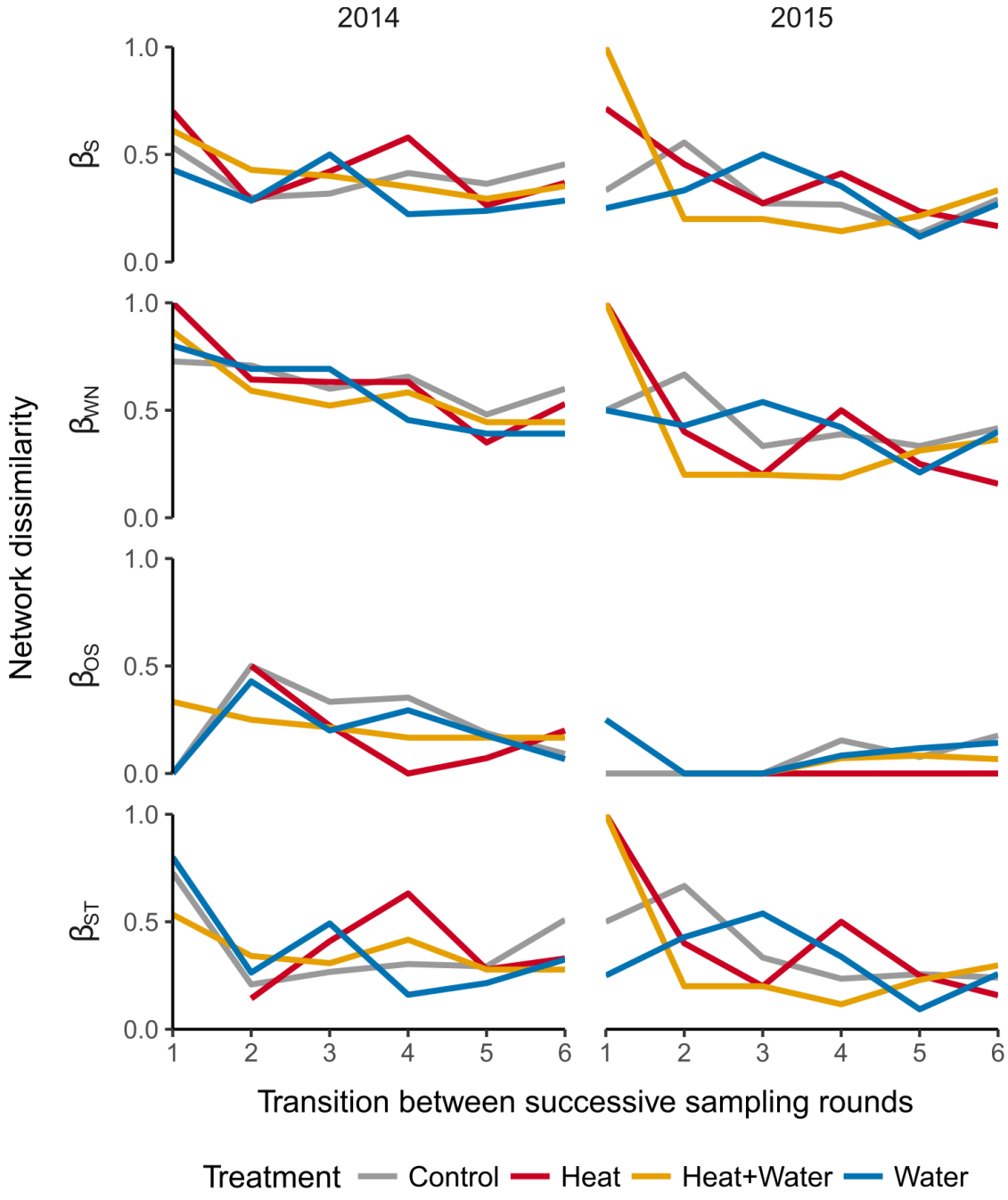


Figure 4.S2 Comparison of the within-season and between-years temporal dynamics for each treatment, using the β_{sim} diversity measure. The x axis represents comparisons of temporally adjacent networks from successive sample rounds. The y axis represents the four different measures of network dissimilarity: β_S is species turnover from one round to the next, β_{WN} is interaction turnover, β_{OS} is the contribution of interaction rewiring to interaction turnover, and β_{ST} is the contribution of species turnover to interaction turnover.

Weather Data

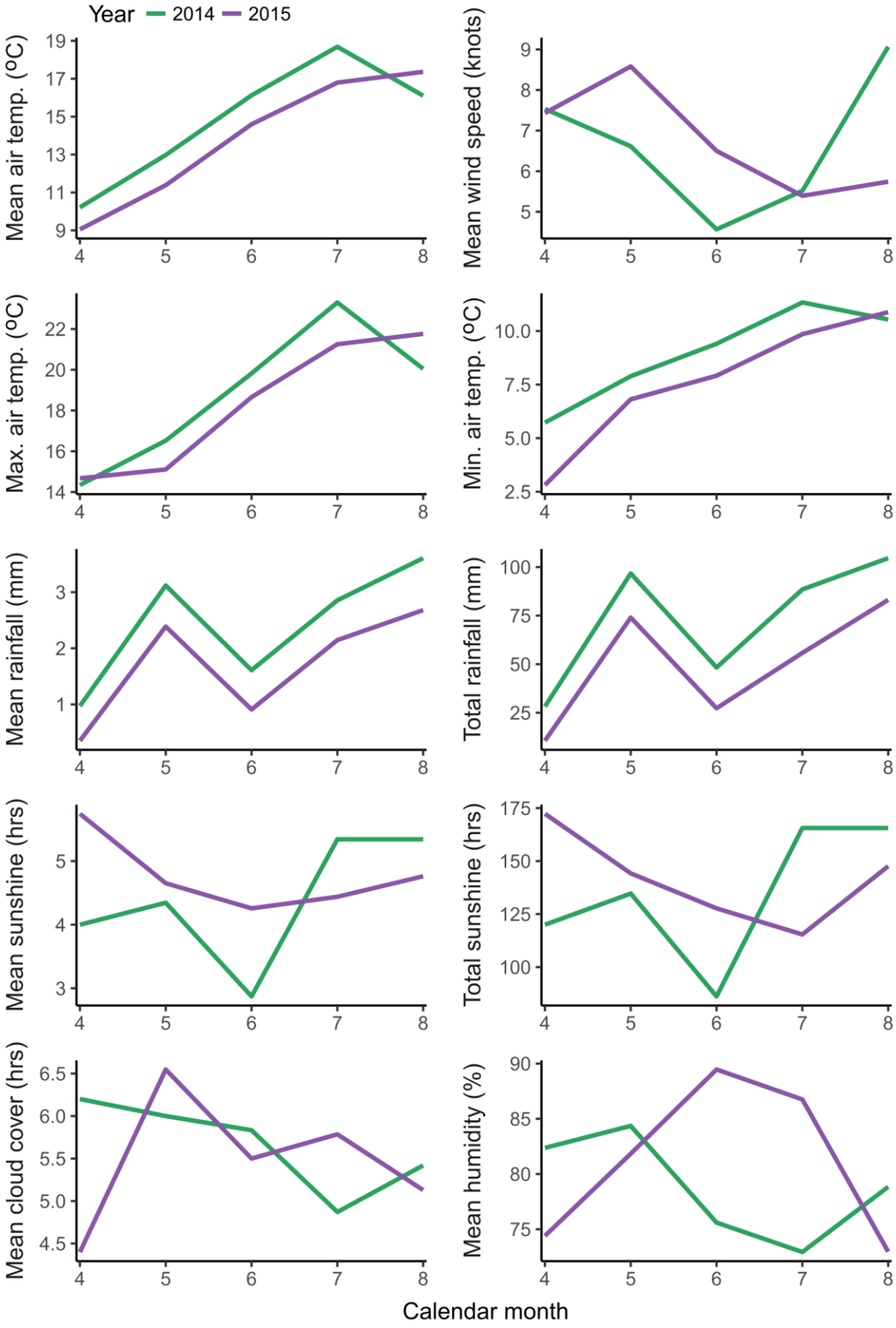


Figure 4.S3 Monthly weather data from the Stockbridge weather station on the field site, from April (month 4) to August (month 8).

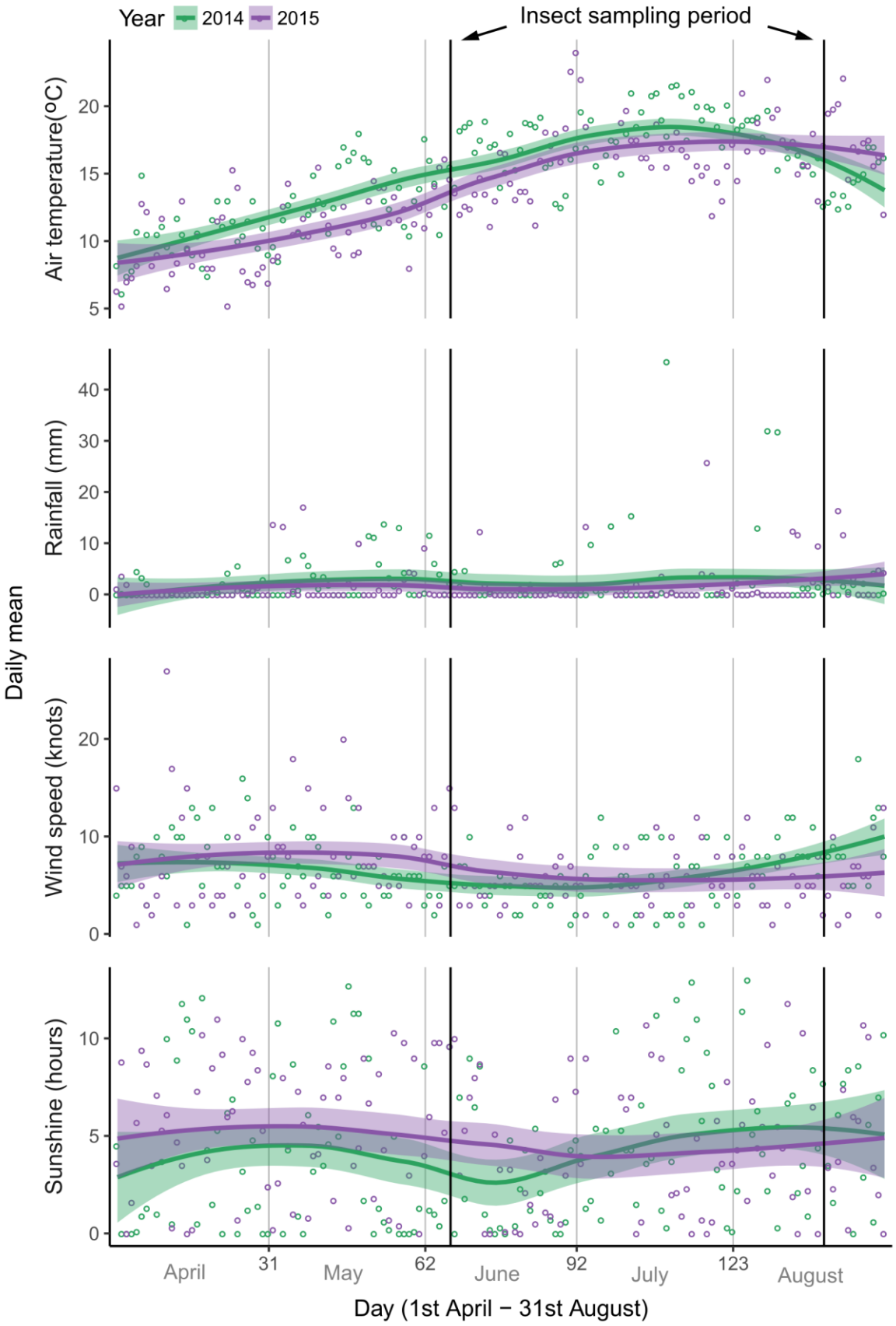
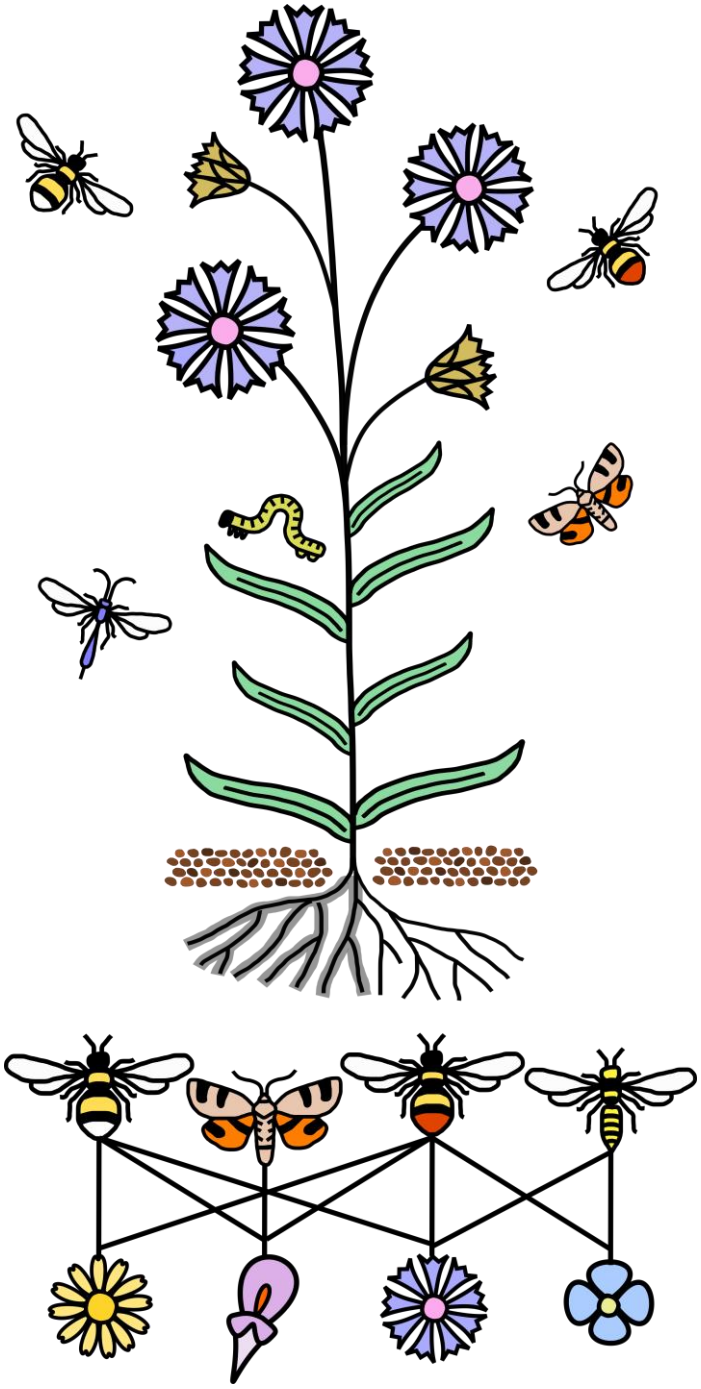


Figure 4.S4 Mean daily air temperature, rainfall, wind speed and sunshine data from the Stockbridge weather station on the field site, from the start of April (day 1) to the end of August (day 153). Grey x-axis gridlines are on the first day of the next month, black vertical lines at days 67 and 141 represent the first and last date of insect sampling respectively.

Chapter 5. General Discussion



5.1 The Impacts of Climate Change on Farmland Biodiversity and Ecosystem Services

In the General Introduction (Chapter 1) I outlined insect-pollinator importance, declines, and current threats, including climate change. My review of the relevant literature highlighted several key areas requiring greater research focus, where novel methodologies and analysis techniques could prove fruitful; the purpose of this thesis is to address some of these areas, and in doing so, contribute to the wider understanding of how climate change may affect plant-pollinator communities and ecosystem services. There were two broad thesis aims; firstly, to develop an interdisciplinary research method that would attempt to provide an overview of the wider impacts of climate change on ecosystem service delivery, by biodiversity, in agro-ecosystems; and secondly, to provide the first experimental evidence of how simulated warming affects plant-pollinator interactions and ecosystem function.

5.1.1 What can we learn from applying a holistic approach?

Because biodiversity loss has ramifications for ecosystem service delivery, there is a need to understand not only how climate change will affect biodiversity, but also how these effects may cascade down to impact human society. Researching climate change from a purely ecological perspective cannot provide a complete picture of the wider impacts; I chose to investigate these wider impacts in Chapter 2 by using and developing the DPSIR framework, a multi-disciplinary approach designed to bridge the science-policy gap (Tscherning et al., 2012), but this novel application also provided the opportunity to assess the effectiveness of the framework in this given context and its ease of use by an ecologist.

The findings from my DPSIR framework application are detailed in Chapter 2, along with the justification for, and description of, the three-step methodology I developed. Viewing the detailed results from the second-step (Figures 2.4-2.6) highlighted several important knowledge gaps within the literature: how will climate change affect species interactions at the level of the community, and could this in turn affect the delivery of ecosystem services? How will reductions in the biodiversity of pollinators, pest regulators, and/or AMF affect non-crop plants? How will climate change affect AMF diversity and abundance? And finally, how will biodiversity loss affect cultural ecosystem service delivery? I went on to address some of these knowledge gaps in Chapters 3 and 4, as discussed below (5.1.2 and 5.1.3). The results of the third-step of the method (Figure 2.7) suggest that the

impacts of climate change on agro-ecosystems will encompass both the physical aspects of the environment, such as soil deterioration, as well as the biological, such as decreases in biodiversity, crop yields, and habitats. All of which points to some potentially serious consequences for humans and society, including: increased soil erosion and carbon emissions, reductions in pollination and pest regulation, reduced food security, and reductions in the health and well-being benefits of interacting with nature.

While the DPSIR framework ultimately proved to be effective, there were some initial questions about how best to employ it in order to achieve the research aims. Almost every single application of the DPSIR to a system or problem in the literature is different in some key way due to the researchers interpreting the framework differently; academics from divergent fields often define the DPSIR categories differently (Gregory et al., 2013; Roura-Pascual et al., 2009), some alter the categories and/or create new ones (Elliott et al., 2017; Kelble et al., 2013), others define common environmental features differently (Bär et al., 2015; Omann et al., 2009) etc. Additionally, there is a great deal of inconsistency within the wider literature regarding ecosystem service definitions and classifications systems (Boerema et al., 2017; La Notte et al., 2017). This diversity of interpretations made it very difficult for me, a trained ecologist but novice in this context, to know where and how the various features of agro-ecosystems should be structured within the framework, and while my decisions were based on logic and proved effective (see 2.4.2 in Chapter 2), they are not likely to be repeated by other researchers. An additional challenge arose when it became evident that I would be unable to explore the climate change impacts with sufficient detail or specificity to meet all of my research aims, at the scale I employed within the initial DPSIR framework; this led me to develop the novel three-step methodology detailed in Chapter 2, which makes the framework more useful for large and complex systems that are responding to environmental change. Future applications could involve examining climate change impacts for protected area networks or coastal habitats and communities, or investigating the wider impacts of pesticide use in agro-ecosystems. However, it is unlikely that other researchers will choose to apply the three-step method developed here, given that most researchers create their own interpretation of the framework by altering the standard format, structure and definitions until they can achieve their aims in one single step. Ultimately, my application of this bespoke DPSIR approach was successful, and while the results from my first data chapter highlighted several knowledge gaps relating to how

communities of interacting species will respond to climate change, I was able to address some of these pertaining to plant-pollinator communities with the investigations in my subsequent data chapters.

5.1.2 How does simulated warming affect pollinators and wildflowers?

In Chapter 3, I presented the findings from my simulated warming experiment, which demonstrated that a relatively modest increase in temperature led to a cascading suite of significant effects that all stemmed from a dramatic decrease in floral abundance and nectar volumes. My results suggest that this striking reduction in floral resources, in turn caused the pollinators to forage from a wider range of wildflower species and visit individual flowers more often. My findings also suggest that, for most of the wildflower species in my experiment, this increased frequency of visits to flowers could not rescue wildflower fecundity from the direct and negative effects of increased temperature.

The results from the simulated warming experiment can begin to answer some of the questions raised by the second-step of the DPSIR analysis. At present, there is very little information in the literature regarding the impacts that climate change could have on the structure and complexity of plant-pollinator interactions in a community-wide context. Studies by Burkle et al. (2013) and Hoiss et al. (2015) both found evidence for changes in network structure that could be linked to climatic changes; the former found warmer conditions to be associated with the loss of specialist pollinators and decreased nestedness, while the latter found colder conditions to be associated with decreased network specialisation. However, given that the study site used by Burkle et al. (2013) experienced land use changes as well as climatic changes, and that Hoiss et al. (2015) used a montane altitudinal gradient as a climate change proxy, the methodological approaches used in these two studies prevent any direct relationships between climate warming and network structure and/or complexity being described. While there are also methodological constraints associated with the experimental approach I employed (see 5.2.2 below), my research can provide clear evidence of simulated climate warming directly impacting network complexity, as I found that a relatively small increase in temperature caused a significant increase in weighted connectance. This increase in connectance cannot be directly attributed to changes in species richness or diet breadth for my experiment, as these were not significantly affected by the simulated warming, though trends were present.

Rather, my findings suggest that plant-pollinator networks are potentially very sensitive to climate change via the cumulative impact of many, potentially subtle, effects that it can have on features such as floral abundance, nectar volumes, species richness, and subsequent changes in visitor foraging behaviour. This point is particularly important because it suggests that investigations of how climate change affects communities, which do not examine species interaction networks, risk missing significant effects and could therefore down-play the impacts and importance of climate change on those communities.

Another important question raised by my DPSIR analysis, was how any changes in community interactions directly affect ecosystem function. My research demonstrated simulated warming had a negative effect on fecundity for the majority of the wildflower species examined, however, I cannot isolate the direct impacts of the heating on the plants from the indirect impacts of the flower visitation. So, while I cannot answer the question of how altered network complexity directly affects seed set, my findings can address the broader question of how the direct and indirect effects of climate warming cumulatively affect wildflower fecundity. Given that increased visitation is linked to increased seed set for some plant species (Garibaldi et al., 2013; Garratt et al., 2014), my research indicates that any positive impacts on fecundity that climate warming may cause via increased visitation, are likely to be outweighed for many plant species by the negative impacts occurring via direct physiological effects. Further to this, two of the four species that experienced reduced seed set under the simulated warming were rare and declining arable habitat specialists (*C. cyanus* and *G. segetum*), while the species that responded positively was a generalist weed (*V. persica*). All of which suggests that climate change may cause permanent shifts in arable plant communities and expedite the loss of declining cornfield annuals, despite potential changes in plant-pollinator network complexity that may otherwise improve fecundity.

5.1.3 How are plant-pollinator temporal dynamics affected by simulated warming?

The flight periods of pollinating insects and flowering periods of wildflowers are often highly seasonal and vary greatly between species; therefore, plant-pollinator communities display temporal dynamism, in which patterns in species abundance, richness, interactions, and turnover can be observed over a variety of time-scales (Basilio et al., 2006; CaraDonna et al., 2017; Olesen et al., 2008; Petanidou et al., 2008). In Chapter 3, I analysed the interaction dataset, generated by the simulated warming experiment, in a temporally

aggregated format in order to boost sample sizes and to provide a consistent sampling scale across the different datasets within that chapter. However, given that previous research agrees on the crucial and overlooked nature of temporal dynamism, I chose to reorganise and expand several of my datasets to conduct a pioneering investigation into how climate warming affects plant-pollinator temporal dynamics. The results of my temporal investigation are detailed in Chapter 4, where I present quite a complicated series of treatment and temporal patterns. However, when these findings are viewed together, they strongly suggest a series of prominent insights; firstly, that plant-pollinator communities demonstrate considerable temporal dynamism, both within and between years; secondly, these dynamics can be significantly disrupted by a relatively small increase in temperature; and thirdly, that these disruptions are mediated by insect community composition and flowering phenology. These findings suggest that climate change impacts on pollinator communities may not only be inconsistent between different communities in different locations, but could also be inconsistent across time for a given community in the same location.

Once again, the results from this investigation directly address some of the questions raised by the second-step of the DPSIR analysis, providing additional layers of detail to those of Chapter 3 (discussed above in 5.1.2). I previously demonstrated that temporally aggregated plant-pollinator networks are susceptible to climate change via the cumulative impact of many effects across the community, including changes in floral resources and foraging behaviour. Given that significant treatment effects on interaction abundance were only found during periods dominated by hoverflies, I can now add to this and state that the susceptibility of these networks to climate change is linked to the wider community composition. Several studies examining historical data have documented that recent climatic changes caused disproportionate losses of specialist pollinator species, when examined over large time-scales, due to their limited capacity to adapt to a changing environment (Bartomeus et al., 2013; Burkle et al., 2013). My findings align with these other investigations and actively demonstrate the mechanism; simulated warming significantly reduced interactions and changed community composition only during periods dominated by hoverflies, but most of the hoverfly species in my dataset were not only generalists in terms of diet and habitat, they are also spatially unrestricted and migratory (Stubbs and Falk, 2002). It is highly likely that these hoverfly individuals simply chose to forage elsewhere,

while the bees were less able to do so, given that they are more spatially restricted and have greater foraging requirements due to offspring provisioning, and that many species are diet specialists (Benton, 2017; Else and Edwards, 2018; Prys-Jones and Corbet, 2011). Thus, it appears that short-term changes in plant-pollinator interactions, temporal dynamics, and community composition can be triggered by raised temperatures during the growing season, which may, somewhat counter-intuitively, lead to temporary losses of generalist pollinator taxa.

The findings of my temporal analysis highlight one further crucial point; the successful detection of changes in plant-pollinator networks and interactions caused by climate warming will be determined by both the sampling and analysis methods. Given that simulated warming only caused significant effects on floral abundance, interaction abundance, and interaction turnover during some of the sample rounds, had I not sampled during those timepoints, my conclusions would be completely different. Therefore, it is extremely important that plant-pollinator interactions and floral data are sampled throughout the entire flowering season when investigating climate change, otherwise important findings could be overlooked. Because I also found striking differences in the responses to simulated warming between the two years, it is also extremely important to sample in more than one year to ensure that variability stemming from community composition can be captured. As previously discussed, the impacts of simulated warming on interaction frequency and community composition were only significant when hoverflies dominated, which would have suggested that other insects are unaffected if I had ended my analysis there. However, I went on to investigate interaction turnover, which demonstrated the opposite pattern as this analysis only revealed strong simulated warming impacts when wild bees were dominant. Once again, this difference in detection is likely due to life history traits; most British wild bee species have shorter flight periods and more specialised floral preferences than British hoverflies, which means that any species turnover due to plant phenological advancement is more likely to facilitate a corresponding turnover of wild bees than it would for hoverflies. Therefore, it is also important to consider the ability of different analysis methods to detect climate change impacts within a given community.

My temporal dynamics investigation, and the research in my other data chapters, successfully applied novel experimental and analytical approaches to answer questions relating to climate change and farmland biodiversity. However, all of my findings should be

viewed in the context of the limitations associated with the various methodologies that I used to generate them.

5.2 Limitations

I previously discussed the specific limitations relating to the methodological approaches employed in each of the data chapters of this thesis (2.4.1, 3.4.1, 4.4.1), but there are also some more general limitations that need to be discussed.

5.2.1 Critique of simulated-warming experiment

There are several limitations inherent to all experiments that simulate climate warming with infra-red heaters in outdoor settings, including that which generated the datasets used in Chapters 3 and 4. Firstly, the linear design of the heating elements that were employed are unable to provide a totally equal temperature difference across the entire perpendicular plot axis, although the radiative shielding housing the elements has been shown to provide relatively even heating across the entire plot (Kimball, 2005). An alternative design of hexagonal heating array employing six ceramic heaters per plot has been developed, and while this new method can provide more consistent heat distribution, it is far more costly to conduct and has not been widely adopted (Kimball et al., 2008). Secondly, heating plots with infra-red heaters creates vapour pressure gradients between leaf interiors and exteriors that are slightly different than would be found under equivalent temperature increases due to climate change, which results in slightly increased rates of transpiration (Kimball, 2005). However, given that climate change is expected to cause changes in precipitation as well as temperature, it is realistic to expect that plants will sometimes experience both heat and drought stress simultaneously, which means that the conditions created by these infra-red heaters are still accurately simulating those that climate change is expected to. Thirdly, the heaters are not very efficient during windy conditions (Kimball, 2005), and while the integrated feedback system ensured that the heaters in my experiment were on as much as was needed to maintain a constant temperature increase, the exposed nature of the site meant that the electricity bill was very high. Another, more general, concern with simulated warming studies is that they underestimate plant responses, both in terms of phenology changes and the greater

susceptibility demonstrated by earlier flowering species (Wolkovich et al., 2012). However, my findings demonstrated a degree of wildflower phenological advancement that tallied with observed changes for wild plants in the UK and I also found that the plant species most strongly affected by the simulated warming, in terms of phenological advancement and interaction turnover, were the earlier flowering species.

5.2.2 Critique of sampling methodology

There are several limitations associated with the flower and insect sampling methods used to collect the datasets analysed in Chapters 3 and 4. Firstly, despite acknowledging that flower-visitation does not necessarily lead to pollination (see section 2.4.2 in Chapter 2), I failed to investigate the effectiveness of the different flower-visitor species at pollinating the plants in my experimental plots. I attempted to assess pollination using a 'single visit deposition' (SVD) experiment, whereby virgin stigma are collected after a single flower-visit (Ballantyne et al., 2015; King et al., 2013), which I ran alongside my climate change experiment. However, the amount of work involved in both conducting the SVD experiment and processing the stigma proved to be too great an addition to my existing workload. Secondly, I am unable to separate the direct effects of simulated warming on plant fecundity from the indirect effects via changes in interactions and community structure. Once again, this is an issue that I foresaw and planned to account for by excluding pollinators from a certain number of flowers per plot, which would then be hand pollinated to arrive at a baseline direct difference. Unfortunately, I was unable to conduct this additional investigation due to the very low floral abundances found in the heated plots; there simply were not enough flowers present to allow sacrificing five or even three from each species, whilst also leaving at least the same number uncovered and allowing the same number to be bagged for nectar analysis. And thirdly, it could be argued that by only sampling during the daytime I could have missed out interactions between the wildflowers and nocturnal flower-visitor species. Nocturnal sampling at an equivalent level of effort as diurnal sampling would have required either a drastic compromise regarding the number of sampling rounds carried out, or an additional full-time researcher focussing on the nocturnal sampling; however, the former option would not have produced a sufficiently robust dataset and the latter was once again beyond the project budget. Additionally, the flowers of most of the species of wildflower in my plots were observed closing during low-light conditions in the evenings and

on very overcast days, which suggests that nocturnal pollination was of limited importance for these species.

5.3 Future Directions

Some of the findings discussed in the preceding data chapters, and in section 5.1 above, naturally lead into some suggestions for future research directions. Additionally, the limitations discussed in this and the previous three chapters (2.4.1, 3.4.1, 4.4.1, 5.2) represent opportunities that future research should aim to address.

5.3.1 Interdisciplinary approaches to science and policy

It is widely acknowledged that there is a need for increased, and more effective, communication between scientists and policy makers (Sutherland et al., 2011, 2004), but the need for increased communication and collaboration between natural scientists and social scientists is equally great (Lowe et al., 2013, 2009). There are two specific research areas highlighted by my DPSIR analysis as currently lacking sufficient direct evidence, which would benefit from an interdisciplinary approach: assessing the importance of specific organism groups, such as pollinating insects, to humans and society; and investigating how biodiversity and habitat loss impact cultural ecosystem service delivery. Investigating these topics would require expertise in both social and natural science, including both qualitative and quantitative data collection and analysis; this combination of skill-sets is unlikely to be found in many ecologists or social scientists, which partly explains the current lack of evidence, and further confirms the need for interdisciplinary approaches. These research areas, which have previously lacked focus, represent opportunities that researchers and funding organisations need to capitalise on; because these topics relate to cultural ecosystem services and human impacts, addressing them would provide an even stronger case to policy-makers for biodiversity conservation and protection of our natural environments.

There are many possible barriers that could prevent interdisciplinary research, ranging from funding difficulties, lack of contact with researchers from other disciplines, lack of skills and knowledge of other disciplines, and use of subject-specific ‘jargon’ and terminologies within the literature. My research highlighted the latter of these in Chapter 2,

where I encountered inconsistent ecosystem service terminologies, definitions, and classification systems between papers written by researchers of different disciplines. The broadly reductionist viewpoint that prevailed in the socio-economic literature provided evidence that was difficult to merge and combine with that of the broadly holistic natural science literature. This barrier could be overcome by attempting to standardise relevant definitions and classifications relating to ecosystem services, but to be successful and widely employed, these standard systems would have to satisfy all relevant disciplines and viewpoints. Arriving at a standardised system of defining and classifying ecosystem services and related processes and benefits may be difficult to achieve if addressed directly, however, it may develop through a more organic process over time provided that interdisciplinary research continues and increases. Additionally, increased collaborations between researchers of different disciplines, within the wider research community, should at least foster a broader understanding of the different terminologies and viewpoints associated with them.

The DPSIR framework I constructed in Chapter 2 drew on evidence from the agricultural, social, economic, and natural science literature, and from various policy documents. While my reasons for selecting this method are sound (see 2.2.2), it could be argued that stakeholder consultation would offer the potential for a stronger verification of both the coverage of the DPSIR framework and the evidence it relies upon. Therefore, it may be prudent to revisit the original research questions and re-create the DPSIR framework, but this time involve other members of the stakeholder community associated with UK agro-ecosystems, ecosystem services, or climate change; if only to demonstrate the validity of the original DPSIR research.

5.3.2 Climate change investigations

My DPSIR analysis highlighted several areas relating to biodiversity and climate change impacts that are lagging behind in terms of research focus and/or research outputs; these areas should be considered research priorities. Firstly, how will climate change affect AMF diversity, abundance and interactions? A handful of studies have demonstrated that increases in temperature can have negative consequences on AMF diversity and spore abundance, but there is very little evidence considering how plant-AMF interactions may be affected (Classen et al., 2015; Shi et al., 2017; Sun et al., 2013). Secondly, how will climate

change affect interactions between pest regulating organisms and insect pests? Very few studies have investigated this topic and those that have used indirect methods or did not examine entire communities (Tylianakis et al., 2008; Zhu et al., 2015). Thirdly, how will any changes in interactions and network structure in plant-AMF and pest regulator-pest communities affect ecosystem service delivery? Once again, there simply is no direct evidence concerning these topics. And finally, how will biodiversity and crop yields be affected by the full range of predicted climatic changes? The vast majority of the studies I included in my DPSIR research investigated climate change by examining only one, or sometimes two, variables, but there is a real need to understand how they will work in concert to affect biodiversity and ecosystem services. These questions are difficult to address due to financial and logistical barriers, but they could be answered through the application of modern sampling techniques and experimental approaches.

Simulated climate change experiments can provide field-realistic evidence of climate change impacts on communities of interacting organisms, but they are an expensive undertaking. Combining temperature increases via infra-red heaters, with CO_2 increases via a free-air CO_2 enrichment system (FACE), is extremely costly; only a handful of studies have so far employed this methodology and all of them have focussed on arable crops (Cai et al., 2015; Ruiz-Vera et al., 2015). The additional need to accurately simulate changes in precipitation that are relevant for the given geographic location is a further complication. Nevertheless, experiments achieving these climate simulations could prove invaluable in answering questions relating to impacts on biodiversity, species interactions, and crop production. There are two important caveats that must be noted however; firstly, future simulated warming experiments must employ a fully factorial design that includes sufficient replicates for statistical power; and secondly, these experiments must also be conducted in a wide range of habitats and coordinated in a way that will facilitate meta-analyses.

The findings from my simulated warming experiment suggest several, more specific, follow-on research projects. My experiment took place in an arable habitat, and whilst I ensured there were sufficient insect-pollinated wildflowers present to investigate plant-pollinator interactions, the crop species grown was a wind-pollinated cereal. The next logical step would be to repeat the experiment with an insect-pollinated crop, such as a dwarf variety of field beans, and to conduct some pollinator-exclusion and hand-pollination techniques; this would allow investigation of not only the direct impacts of simulated

warming on crop yields, but also the indirect impacts via any changes in species interactions. Another clear follow-on for this experimental design would be to use it to investigate plant-pollinator interactions in semi-natural habitats, such as wildflower-rich grasslands or perennial meadows; this would allow investigation of changes in more natural communities, over longer timescales, and with continuous heating. My research also suggests a future project that would require a different experimental approach; many of my results appear to demonstrate that different pollinator groups respond to simulated warming differently, which should be further investigated using some closed-system experiments. The findings of my simulated warming experiment indicate one further point regarding future climate change investigations; to ensure that the full scope of the impacts across the entire plant-pollinator community are captured, species interactions must be examined.

5.3.3 Species interaction networks

My findings suggest several specific areas requiring future investigation with a network approach and also point to several emerging and developing techniques that should improve our understanding of these, and other, areas of research. The most striking knowledge gap highlighted by my DPSIR analysis is the almost complete absence of evidence documenting if, and how, changes in community interactions and structure affect ecosystem service delivery. It is essential that these relationships are clarified along the entire causal chain, to provide a more complete picture of how environmental change may affect ecosystems and the services they provide. Investigating these relationships directly could be achieved through a wide variety of experimental designs, including; open-system community manipulations via a partial-exclusion mechanism, such as mesh or netting too fine to permit all species of pest regulator or pollinator; open-air simulations of environmental change, such as the climate warming experiments suggested in the previous paragraph; and closed-system experiments comparing the performance of different communities, which allow greater control at the potential expense of validity. However, my DPSIR analysis also highlighted that identifying species and directly measuring interactions can be particularly challenging for some groups, such as AMF and parasitoid insects, and time and labour intensive for others, such as pollinators. Fortunately, advances in DNA metabarcoding should enable easier and faster identification of species and interactions (Evans et al., 2016). This technique will also allow direct measurement of interactions in some contexts, including

insect parasitoids and AMF, which could be combined with direct measurement of ecosystem service/function; this would permit easier exploration of the link between community interactions and ecosystem service. However, DNA metabarcoding can only provide indirect measurement of interactions for some organisms, such as insectivorous birds (via faecal samples) and pollinating insects (via pollen swabbing of trap-caught individuals), which then makes it far more challenging to establish a direct link to service provision. An additional caveat with barcoding based approaches is their limited ability to pinpoint exactly when an interaction occurred, which may constrain their use for investigations relating to phenology and could obscure any fine-scale temporal dynamics that the community displays.

The substantial temporal variation that occurred right across the plant-pollinator community in my simulated warming experiment, both within and between years, strongly suggests that all future investigations of plant-pollinator interactions must consider the temporal dynamics of the system in question; this is especially crucial for investigations relating to environmental change. At present, there is no standard approach for analysing network temporal dynamics, either in terms of chronological scale or analysis. While the temporal scale is partially determined by the context of the research question(s), it would be advisable to sample at the finest resolution possible, so as to preserve as much detail as can be collected within the raw dataset. Both the relevant literature and my own results indicate that temporal analysis must include an assessment of interaction turnover, as well as other features of the community (CaraDonna et al., 2017; Olesen et al., 2008), which has been achieved by myself and others via sequential comparisons using diversity indices (Burkle and Alarcón, 2011; CaraDonna et al., 2017). Another possible method of incorporating temporal assessment into network analysis could be found in the currently developing field of 'multilayer networks', which can create and analyse more spatially and temporally sophisticated networks thanks to the far more detailed underlying data structure (Pilosof et al., 2017). All interaction networks are built using an 'edge list' (list of interactions), but those of multilayer networks incorporate additional information, which could include interaction-specific data relating to time, location, mutualism/antagonism etc. This additional information is used to create separate, but linked, layers of networks, which could allow many different network features to be examined more quickly and easily, all using the same datafile. There are undoubtedly numerous other experimental, technical, and

analytical approaches currently being developed that will facilitate the answering of many ecological questions relating to environmental change, including those highlighted by my thesis.

5.4 Conclusions

Throughout this thesis, I have demonstrated that climate warming has the capacity to cause significant, community-wide impacts on wildflowers and pollinating insects in agro-ecosystems. I have documented the potential for negative consequences to cascade across the community and wider ecosystem; starting with decreases in floral resources and phenological advancement; which caused reductions in interaction frequency and advanced patterns in interaction turnover; decreases in wildflower fecundity (especially for rare habitat specialists) followed next; all of which could finally lead to reductions in the delivery of both pollination and cultural ecosystem services. There are still many questions relating to climate change and its impact on communities and ecosystem services that remain unanswered, but doing so, with novel experiments and analyses and interdisciplinary research, will provide a stronger case for biodiversity conservation and ecologically-based management of our agro-ecosystems.

5.5 References

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